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JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

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Fisheries Research Board of Canada
Office of the Editor
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Glycogen and Lactic Acid Concentrations in Atlantic Cod (*Gadus morhua*) in Relation to Exercise[1]

By F. W. H. Beamish[2]

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

In Atlantic cod, muscle glycogen was reduced by about 50% at moderate swimming speeds and over 80% at higher speeds. Muscle glycogen for a given swimming speed was generally lower after 30 min exercise than after 15 min exercise. During the 8-hr period after strenuous exercise, muscle glycogen increased but remained well below the level for unexercised fish.

At moderate swimming speeds, fish exhibited comparatively small amounts of muscle and blood lactic acid. At higher swimming speeds, fish accumulated significantly larger quantities of lactic acid in the muscle and blood. During the recovery period after strenuous exercise, muscle and blood lactic acid increased precipitously. Muscle lactic acid remained high for 1 hr after exercise and then decreased in 8 hr to levels similar to those of unexercised cod. Blood lactic acid followed a similar pattern except that it continued to increase for 1.5 hr after exercise.

Serial samples of blood taken before and after 30 min strenuous exercise showed marked differences in lactic acid among individuals. Blood lactic acid usually continued to increase for 30–60 min after exercise, and decreased to the level for unexercised fish about 24 hr after exercise.

No mortalities attributable to muscular fatigue occurred among cod.

INTRODUCTION

Changes in carbohydrate metabolism in fish after severe muscular exercise are well documented (Black, 1957a, b, c; Heath and Pritchard, 1962; Black et al., 1962; Wendt, 1965; and others). During strenuous activity, muscle glycogen, likely the main fuel for muscle metabolism, is reduced to lactic acid. Muscle lactic acid diffuses to the blood (Nakatani, 1957; Black et al., 1962). Appreciable concentrations of lactic acid may persist in the blood for many hours after exercise (e.g., Black, 1955; and Heath and Pritchard, 1962).

In at least three instances a correlation between high blood lactic acid and mortality has been demonstrated after exercise (Parker et al., 1959; Beamish, 1966b; Caillouet, 1967). The actual cause of death is uncertain. Suggested explanations include interference with the acid base equilibrium coupled with reduced affinity of haemoglobin for oxygen, and, in the presence of excess acid, reduced affinity for carbon dioxide (Black, 1958).

Particularly little information is available on the intensity and duration of exercise necessary to alter the levels of muscle glycogen and lactic acid. Often in fatigue studies duration of exercise and speed of swimming are either not controlled or not reported. Frequently in laboratory studies, fish are exercised until they lose equilibrium or in some other way demonstrate fatigue.

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[1]Received for publication October 16, 1967.
[2]Present address: Department of Zoology, University of Guelph, Guelph, Ont.

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In field studies, where exercise consists of capture by commercial gear, swimming speed and duration of exercise may be difficult to hold constant or even estimate. Thus coho salmon, *Oncorhynchus kisutch*, were landed between 1 and 30 min after hooking (Parker et al., 1959). Capture of haddock, *Melanogrammus aeglefinus*, by otter trawl could have occurred at any time during a 30-min tow (Beamish, 1966b).

To increase information on the influence of swimming speed and exercise period on utilization of muscle glycogen, and on production of muscle and blood lactic acid, a study was made on Atlantic cod, *Gadus morhua*.

MATERIALS AND METHODS

Cod were captured by otter trawl in Passamaquoddy Bay in the Bay of Fundy. All tows were made by the research vessel, M.B. *Mallotus*, with a small otter trawl having a footline of about 15 m and a headline height of 2 m. The gear was towed along the sea bed at 140 cm/sec for 30 min. Tows were made only during April through August and at depths from 45 to 55 m. During this period bottom temperatures varied from 4 to 10 C.

After capture, cod were held aboard the research vessel in tanks 1 m in diam by 0.7 m in depth. Water flow was adjusted to maintain dissolved oxygen at or near air saturation. Temperature in holding tanks was within 2.7 C of that near bottom. At the laboratory, cod were transferred to holding tanks 2 m in diam by 1.3 m in depth. Temperature was regulated to that in the research vessel's tanks. Oxygen was near air saturation. Fish were fed a mixture of beef liver and herring. After they began to feed, water temperature was increased by 1 C per day until the experimental temperature, 13 C, was reached. Fish were held for at least 4 weeks at 13 C before being used in experiments.

Cod were exercised in either of two chambers. The chamber used in 1963, when serial blood samples were taken from individual fish, was essentially an oval-shaped trough in which water was circulated in a clockwise direction (Fig. 1). Baffles were installed ahead of the swimming chamber to reduce turbulence. Water velocity was regulated by a variable speed centrifugal

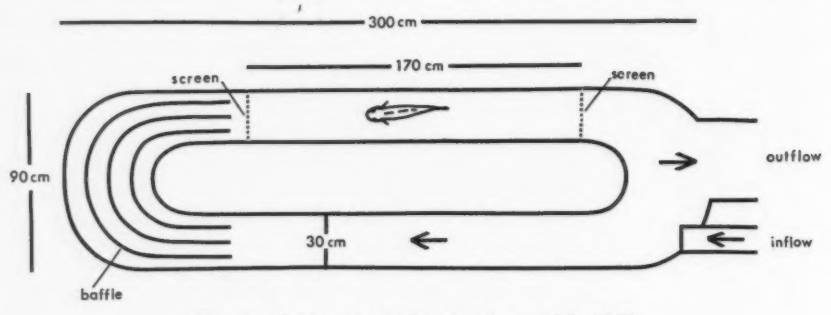

FIG. 1. Design of exercise chamber used in 1963.

pump. In 1964 and 1965, experiments were conducted in a second activity chamber which was modelled after that described by Blazka et al. (1960), except that an open system was used. A cylindrical acrylic chamber, appropriately baffled, was immersed in an open bath (Fig. 2), as described in Beamish (1966a). Water velocity in the chamber was regulated by a propeller driven by a variable speed $\frac{3}{4}$ hp Zero Max motor and was measured with an Ott current meter, model Arkansas. In both chambers maximum water velocity was 130 cm/sec.

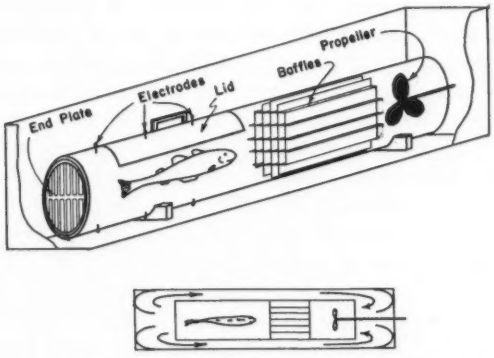

FIG. 2. Design of activity chamber used in 1964 and 1965. Arrows indicate direction of flow. Length of the cylinder is 107 cm and the inner diam is 16.5 cm. The length of chamber available to a fish is 65 cm.

Usually blood samples were taken by cardiac puncture with a heparinized 2-ml syringe lubricated with paraffin oil. However, for serial samples from an individual fish, blood was obtained from the dorsal aorta in the region of the caudal peduncle. In the determination of blood lactic acid, cold trichloroacetic acid was used to deproteinize blood. The mixture was filtered and the filtrate processed according to the method of Barker and Summerson (1941). Lactic acid concentration was expressed as milligrams of lactic acid per 100 ml of whole blood.

Muscle samples were taken from the epaxial muscle immediately below the first dorsal fin. A sample, 10–15 g, was removed quickly, placed in 60 ml of cold 3% perchloric acid, weighed, and homogenized for 3 min (D. I. Fraser, personal communication). The mixture was filtered and the filtrate volume adjusted with perchloric acid to 100 ml. Glycogen was precipitated with ethanol according to Carroll et al. (1956). Phenol and sulphuric acid were used for colour development (Montgomery, 1957). Muscle glycogen was expressed as milligrams of glycogen per 100 g of muscle (wet weight). Recent studies by Fraser et al. (1966) suggest that the method of glycogen determination followed in this study yields lower values than the extraction method

using potassium hydroxide. Muscle lactic acid was estimated by the method outlined in Hawk et al. (1947), and expressed as milligrams of lactic acid per 100 g of muscle (wet weight).

Fish were placed in an activity chamber about 12 hr before exercise was begun to eliminate effects of handling. Dissolved oxygen level in the chamber was near or at air saturation. To exercise a fish, water velocity was slowly but steadily increased to the desired speed. Gentle prodding was used sometimes to induce fish to swim. Fish were exercised in the morning and only during the summer months to reduce possible influence of diel and seasonal fluctuations in metabolism on the concentration of glycogen and lactic acid. After the experimental conditions of exercise or of recovery after exercise were satisfied, the fish was removed and 0.5 ml of blood withdrawn. Immediately afterwards, the fish was stunned by a sharp blow on the head, and a muscle sample was excised. Weight, total length, and sex were then determined. Otoliths provided an estimate of age. Generally, each fish was sampled once. However, for one experiment, blood samples were taken from each fish before exercise and at regular intervals for 12 hr after exercise.

Unless otherwise stated fish were fed 12 hr before exercise was begun. As often as practicable fish of similar size were used for a given experiment. Usually fish were about 40 cm in total length. Larger fish were used when serial blood samples were withdrawn from an individual. In another experiment, where lactic acid concentration was measured in unfed fish after exercise, only larger cod were available.

Changes in lactic acid and glycogen in relation to swimming speed were tested for significance by an analysis of variance (Snedecor, 1948). Logarithmic transformations were used to reduce variance. Duncan's 5% multiple range test (Steel and Torrie, 1960) was used to compare logarithmic means. Standard errors were calculated for lactic acid, glycogen, and total length (Stanley, 1960). Differences in lactic acid and glycogen concentrations between males and females under comparable conditions of exercise or recovery after exercise were examined by a chi-square test (Snedecor, 1948) and in all cases found not to be significant at $P = 0.05$.

RESULTS

Unexercised Cod

Cod, maintained in individual tanks, were anaesthetized with 2-phenoxyethanol before sampling. Glycogen was 272 mg/100 g and blood lactic acid 21.2 mg/100 ml (Fig. 3, Table I). Muscle and blood lactic acid for cod not anaesthetized before sampling were 66.8 mg/100 g and 12.9 mg/100 ml. An analysis of variance indicated blood lactic acid concentrations for the two treatments were significantly different ($P = 0.05$). During anaesthesia, circulatory efficiency might be impaired, with consequent hypoxia and lactic acid production. Hence, the blood lactic acid concentration for fish not anaesthetized was taken to represent the unexercised condition.

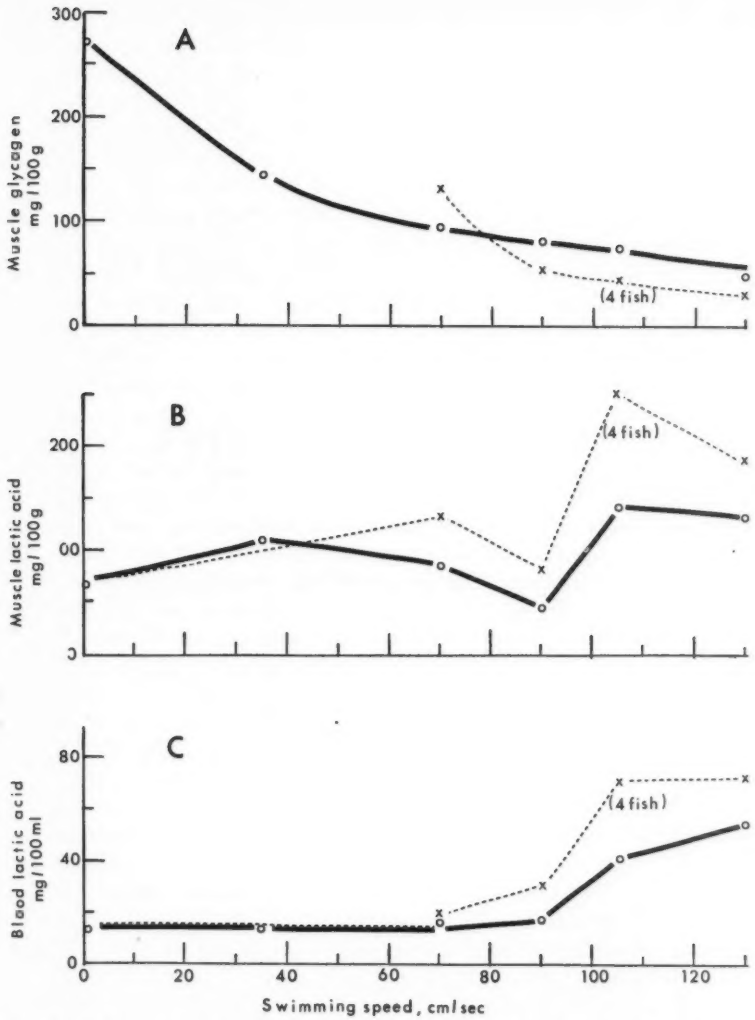

FIG. 3. Influence of swimming speed and duration of exercise on muscle glycogen and muscle and blood lactic acid of Atlantic cod. Open circles represent values after 15 min exercise, X's, values after 30 min exercise (10 fish except as indicated).

EXERCISED COD

Muscle glycogen decreased rapidly from 272 mg/100 g for the unexercised condition to 142 mg/100 g after 15 min exercise at 35 cm/sec (Fig. 3A, Table I). With increase in swimming speed, glycogen continued to decrease but at a lower rate. After 15 min exercise at 130 cm/sec, glycogen was 48 mg/100 g,

TABLE I. Mean values for muscle glycogen, muscle lactic acid, and blood lactic acid of cod, *Gadus morhua*, with variation in swimming speed and duration of exercise. Temperature 13 C.

Swimming speed (*cm/sec*)	Mean length (*cm*)	Mean weight (*g*)	No. of fish			Age (*years*)	Muscle glycogen (*mg/100 g*)	Muscle lactic acid (*mg/100 g*)	Blood lactic acid (*mg/100 ml*)
			Total	♂	♀				
No exercise									
0	56.2±4.6[a,b]	1949	12	7	5	3–5	272±34	–	21.2±7.0
0	39.0±4.0[c]	552	16	8	8	3	–	66.8±7.2	12.9±4.6
15 min exercise									
35	41.8±1.3	734	10	6	4	3	142±36	109.8±15.2	13.0±3.2
70	39.3±1.5	609	10	3	7	3–4	98±22	87.3±12.0	16.9±3.2
90	36.8±1.3	480	10	4	6	3–4	80±34	47.1±9.1	17.9±3.2
105	40.6±0.8	676	10	8	2	3–4	75±22	143.6±23.8	42.4±6.3
130	38.5±1.0	574	10	2	8	3–4	48±38	133.6±16.6	55.3±2.4
30 min exercise									
70	40.7±0.7	623	10	4	6	3	130±13	135.2±15.4	19.8±2.7
90	41.2±1.4	702	10	4	6	3–4	53±24	83.6±14.2	30.9±6.8
105	38.8±3.8	608	4	0	4	3	45±32	253.1±40.6	71.4±15.6
130	40.9±3.3	673	10	6	4	3	30±28	189.0±20.4	72.9±3.3

[a]Two standard errors.
[b]Fish anaesthetized.
[c]Fish not anaesthetized.

one-sixth of that before exercise. Duncan's multiple range test indicated that muscle glycogen for unexercised cod was significantly higher in concentration than for exercised fish at all swimming speeds except 35 cm/sec. Glycogen concentrations at 70 and 105 cm/sec were not significantly different from that at 35 cm/sec. At the highest swimming speed tested, 130 cm/sec, glycogen was significantly lower than at all speeds except 90 cm/sec.

Similarly, in cod exercised for 30 min, muscle glycogen decreased with increase in swimming speed (Fig. 3A, Table I). However, significant differences in glycogen were not demonstrable among the swimming speeds tested. For comparable swimming speeds, glycogen generally was lower after the longer exercise period, the one exception being at 70 cm/sec. But significant differences between the two exercise periods were not found for any of the swimming speeds.

Muscle lactic acid after 15 min exercise at 35 cm/sec was almost twice as high as for unexercised fish (Fig. 3C and Table I). A decrease to about the unexercised concentration occurred between 35 and 90 cm/sec. With further increase in swimming speed to 105 cm/sec, lactic acid rose sharply but between 105 and 130 cm/sec the concentration declined slightly. Significant differences in lactic acid were not demonstrable among the swimming speeds tested except at 90 cm/sec, where the lowest concentration was found.

The patterns of the relation between swimming speed and muscle lactic acid were similar for the two exercise periods. Significant differences in muscle lactic acid after 30 min exercise were not found among the different swimming speeds. Between the two exercise periods, lactic acid was significantly higher after 30 min at 90 and 105 cm/sec and lower after 15 min at 130 cm/sec.

Blood lactic acid in fish after 15 min exercise at swimming speeds to 90 cm/sec did not differ significantly from the unexercised concentration (Fig. 3C, Table I). A prominent increase in blood lactic acid occurred at higher swimming speeds. At 105 cm/sec, lactic acid was 42.4 mg/100 ml, significantly higher than concentrations at lower swimming speeds. Lactic acid was higher in concentration at 130 cm/sec than at 105 cm/sec; however, a significant difference was not demonstrable. The pattern of the relation between blood lactic acid and swimming speed after 30 min exercise was similar to that after the shorter exercise period. For comparable swimming speeds, blood lactic acid was higher after the 30 min exercise period, but significant differences were observed only at 105 cm/sec.

Recovery after Strenuous Exercise

For cod fed 12 hr prior to an experiment, muscle glycogen decreased precipitously from the unexercised concentration of 272 to 30 mg/100 g immediately after 30 min exercise at 130 cm/sec (Fig. 4A, Table II). Comparatively little change in glycogen was observed 1 hr after exercise. Thereafter glycogen concentration increased to 117 mg/100 g after 8 hr recovery, almost half that for unexercised cod.

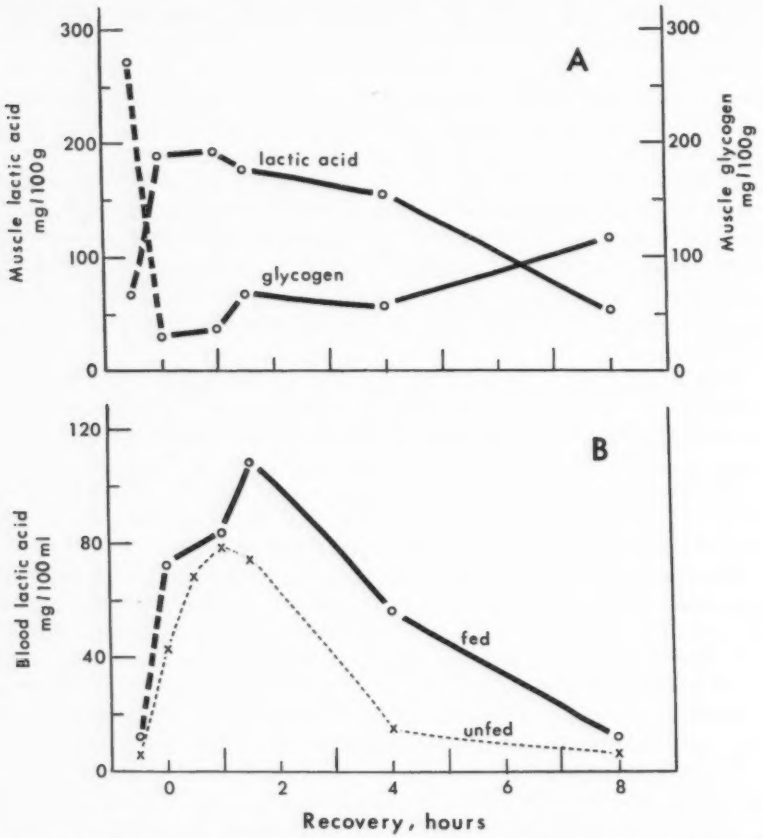

FIG. 4. Values for muscle glycogen and blood and muscle lactic acid before and after 30 min exercise at 130 cm/sec. Open circles represent values for 10 fish fed 12 hr prior to exercise, ×'s, 6–13 fish unfed for 72 hr before exercise.

Muscle lactic acid increased from the unexercised level of 66.8–189.0 mg/100 g immediately after exercise (Fig. 4A, Table II). It remained unchanged for 1 hr and then decreased, reaching unexercised levels 8 hr after exercise.

Blood lactic acid increased in concentration from 17.0 mg/100 ml before exercise to 72.9 mg/100 ml immediately after exercise (Fig. 4B, Table II). The increase continued for 1.5 hr, when the concentration was 108.1 mg/100 ml. The concentration then declined, reaching unexercised levels at 8 hr.

For cod unfed for 72 hr and then exercised for 30 min at 130 cm/sec, blood lactic acid during recovery followed a pattern (Fig. 4B, Table II) similar to that for the more recently fed cod. However, for comparable intervals after

TABLE II. Mean values for muscle glycogen and muscle and blood lactic acid in starved and fed cod sampled after 30 min exercise at 130 cm/sec. Temperature 13 C.

Recovery period (*hr*)	No. of fish			Mean length (*cm*)	Mean weight (g)	Muscle glycogen (*mg/100* g)	Muscle lactic acid (*mg/100* g)	Blood lactic acid (*mg/100 ml*)
	Total	♂	♀					
Fed within 12 hr								
0	10	6	4	40.9±1.0[a]	673	30±28	189.0±20.4	72.9±3.3
1.0	10	3	7	39.2±1.0	552	38±14	192.4±32.7	84.1±12.8
1.5	10	5	5	39.1±0.8	532	67±24	176.1±28.4	108.1±22.3
4.0	10	4	6	38.3±1.0	521	57±24	153.7±29.4	58.5±22.2
8.0	10	3	7	40.0±0.5	581	117±12	52.9±5.8	11.7±2.4
Unfed for 72 hr								
0[b]	13	4	9		1085			5.8±0.9
0	8	4	4		994			52.6±5.9
0.5	9	5	4		927			67.7±10.1
1.0	8	6	2		1414			79.3±8.0
1.5	8	4	4		1147			74.2±8.2
4.0	6	3	3		1119			15.6±5.3
8.0	6	4	2		1048			6.2±2.3

[a]Two standard errors.
[b]Before exercise.

exercise, lactic acid was lower among the unfed cod but significantly so only at 240 and 480 min recovery. Further, among unfed fish, maximum lactic acid accumulation occurred one hr after exercise was terminated, 30 min earlier than that found for recently fed cod.

Serial Measurements of Blood Lactic Acid in Individual Fish

In serial measurements of blood lactic acid for 10 cod before and after 30 min exercise at 130 cm/sec, marked differences occurred among individuals (Fig. 5, Table III). But for most fish, the patterns of the relation between lactic acid accumulation and recovery after exercise were similar and consistent with that in Fig. 4B. Immediately after exercise blood lactic acid was much higher than for the unexercised condition. Maximum levels of lactic acid among surviving fish occurred within 4 hr of recovery and ranged between 40 and 100 mg/100 ml. For most survivors lactic acid did not return to unexercised levels until 24 hr of recovery. Three of the 10 cod died during recovery (two within 5 hr, one after 24 hr). Lactic acid was not measured at death.

DISCUSSION

Among vertebrates, muscle glycogen is generally considered the most conveniently stored and readily utilizable source of energy to support strenuous muscular activity. Cod utilized about 82% of muscle glycogen during 15 min exercise at 130 cm/sec. Even at moderate swimming speeds, a notable decrease in glycogen was observed. In contrast, blood lactic acid did not change appreciably from the unexercised level over the lower swimming speeds. Muscle lactic acid varied considerably at moderate swimming speeds, tending to decrease with increase in swimming speed. At swimming speeds above 90 cm/sec, both muscle and blood lactic acid were much higher than at lower speeds.

If it can be assumed that more muscle lactic acid would be produced as more glycogen were degraded, then this lactic acid was apparently more efficiently oxidized as swimming speed increased through 90 cm/sec, perhaps as a result of improved circulatory efficiency. As swimming speed increased further, oxygenation of the tissues apparently could not keep pace with the production of lactic acid which accumulated in muscle and blood, and glycogen continued to be degraded.

Generally, depletion of muscle glycogen and accumulation of lactic acid in cod were greater after the longer exercise period and most pronounced at the higher swimming speeds. Concordant with these observations, Black et al. (1962) found a 50% reduction in muscle glycogen in rainbow trout after 30 min of moderate exercise and 84% after 15 min of strenuous exercise. Hammond and Hickman (1966) observed four- and five-fold increases in muscle and blood lactic acid in rainbow trout after moderate exercise for short periods. Nakatani (1957) found a two-fold increase in lactic acid of rainbow trout after a short period of severe exercise.

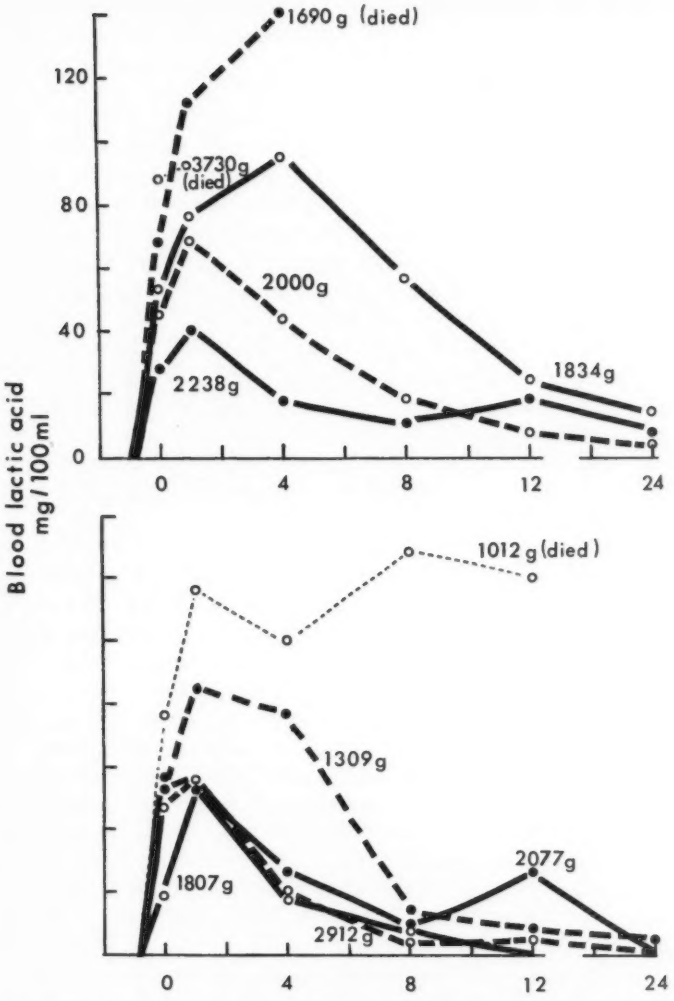

FIG. 5. Values for blood lactic acid for individual Atlantic cod sampled before and at regular intervals after 30 min exercise at 130 cm/sec.

Changes in muscle glycogen in cod during recovery from strenuous exercise followed a pattern similar to that demonstrated for other species subsequent to strong exercise. Glycogen levels in cod after exercise remained well below unexercised levels over an 8 hr recovery period. Similar observations have been made for rainbow trout by Black et al. (1962) and for Atlantic salmon by Wendt (1965). Black et al. (1962) suggest that replacement of muscle glycogen is dependent on absorption of food from the alimentary tract.

TABLE III. Values for blood lactic acid of individual cod before and at regular intervals after 30 min exercise at 130 cm/sec. Temperature varied between 13.5 and 14.0 C.

Date (1963)	Temp (*C*)	Weight (*g*)	Sex	Age (*years*)	Blood lactic acid (*mg/100 ml*)						
					Unexercised	Recovery (*hr*)					
						0	1	4	8	12	24
Aug. 9	13.5	2000	♂	4	2.9	44.9	68.1	43.2	18.5	7.6	3.8
12	14.0	1690	♂	4	7.5	67.9	112.6	141.7	Died between 4 and 8 hr		
12	14.0	1834	♂	4	5.7	53.1	76.5	95.0	57.1	24.2	13.8
13	14.0	2238	♀	4	10.0	28.3	39.9	18.5	10.0	18.4	7.0
13	14.0	1309	♂	3	7.9	53.0	85.0	76.3	14.5	7.8	5.0
14	14.0	1807	♂	4	3.3	18.7	53.1	17.1	8.0	0.7	0.9
14	14.0	1012	♀	3	2.5	76.5	115.5	100.8	128.5	121.1	Died between 12 and 24 hr
15	14.0	2912	♂	4	0.7	46.9	55.0	20.7	3.3	5.3	2.9
16	14.0	2077	♂	4	0.7	56.8	52.5	25.7	8.8	26.8	3.0
17	14.0	3730	♀	4	–[a]	89.0	93.9	Died at 1.5 hr			

[a]Sample not taken.

In accord, Wendt (1965) observed a more rapid replenishment of muscle glycogen after exercise if fish were fed.

That muscle lactic acid in cod immediately after cessation of strenuous swimming was much higher than in unexercised fish is in accord with observations of Nakatani (1957), Black et al. (1962), and Hammond and Hickman (1966) on rainbow trout. The gradual disappearance of muscle lactic acid in cod during recovery is in general agreement with observations by Black et al. (1962) on rainbow trout. Blood lactic acid in cod increased after severe exercise and, in contrast to the pattern followed by muscle lactic acid, continued to increase during the first hour and a half of recovery before subsiding to unexercised concentrations some hours later. Similar alterations in blood lactic acid after strenuous swimming have been demonstrated for other species by Black (1957 a, b, c), Black et al. (1961), Wendt (1965), and Hammond and Hickman (1966). The lag in time of occurrence of maximum concentrations of muscle and blood lactic acid reflects the slow rate of diffusion of lactic acid from muscle to blood. Suggestions to explain the delay in disappearance of blood lactic acid after exercise include impaired circulation, slow rate of diffusion, and limitations of the respiratory system (Black et al., 1961).

Comparison of levels of blood lactic acid reported for different species is difficult because duration of exercise is not standard (Beamish, 1966b). Further, it is often difficult to assign qualitative values to intensity of exercise and physical condition of fish. Nevertheless there is striking similarity in the patterns of lactic acid after strong exercise. Customarily, blood lactic acid increases from two- to about 13-fold immediately after exercise (Beamish, 1966b). In cod, the increase was about four-fold. The recovery period required to reach maximum concentration of lactic acid varies considerably among species as does concentration. For example, a maximum concentration of 22 mg/100 ml was found for carp immediately after exercise by Caillouet (1964). In contrast, chinook salmon reached maximum levels of 196 mg/100 ml between 210 and 240 min after capture (Parker and Black, 1959). Maximum concentration for cod, 108.1 mg/100 ml, occurred 90 min after exercise. For most species including cod, lactic acid returns to unexercised levels within 16 hr recovery.

Post-exercise levels of blood lactic acid were lower for cod unfed for 72 hr prior to an experiment than for fish fed within 12 hr. Muscle glycogen levels were not measured but may have been lower in the unfed cod. Black et al. (1960) observed a reduction in muscle glycogen with starvation among unexercised rainbow trout. Lower levels of glycogen among unfed cod could account for the lower levels of blood lactic acid during recovery. On the other hand, lower levels of lactic acid among unfed cod may reflect greater availability of oxygen for oxidation of lactic acid. Metabolic expenditure is lowered considerably in unfed fish because of reduced expenditure for assimilation of food. Beamish (1964) observed a 50% reduction in resting oxygen consumption of brook trout, *Salvelinus fontinalis*, and white sucker, *Catostomus commersonii*,

after 2 days' starvation. Similar reduction in oxygen uptake with starvation was recorded for aholehole, *Kuhlia sandvicensis*, by Muir et al. (1965).

Changes in blood lactic acid of individual fish after strenuous exercise followed patterns similar to that established for large numbers of fish each sampled once. Usually blood lactic acid for individuals repeatedly sampled required a longer recovery to subside to unexercised levels. This is attributed to repeated capture and handling of cod during serial sampling. It is well documented that capture and handling of fish raises the level of lactic acid (e.g., Black, 1956; Wendt, 1965).

Few mortalities were observed among cod during recovery from severe exercise. All mortalities that occurred were among individuals subjected to serial sampling. Here internal difficulties might have arisen from frequent sampling and directly or indirectly caused death.

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REFERENCES

BARKER, S. B., AND W. H. SUMMERSON. 1941. The colorimetric determination of lactic acid in biological material. J. Biol. Chem., **138**(2): 535–554.

BEAMISH, F. W. H. 1964. Influence of starvation on standard and routine oxygen consumption. Trans. Am. Fish. Soc., **93**(1): 103–107.

1966a. Swimming endurance of some Northwest Atlantic fishes. J. Fish. Res. Bd. Canada, **23**(3): 341–347.

1966b. Muscular fatigue and mortality in haddock, *Melanogrammus aeglefinus*, caught by otter trawl. Ibid., **23**(10): 1507–1521.

BLACK, E. C. 1955. Blood levels of haemoglobin and lactic acid in some freshwater fishes following exercise. J. Fish. Res. Bd. Canada, **12**(6): 917–929.

1956. Appearance of lactic acid in the blood of Kamloops and lake trout following live transportation. Canadian Fish Culturist, **18**: 20–72.

1957a. Alterations in the blood level of lactic acid in certain salmonid fishes following muscular activity. I. Kamloops trout, *Salmo gairdneri*. J. Fish. Res. Bd. Canada, **14**(2): 117–134.

1957b. Alterations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. II. Lake trout, *Salvelinus namaycush*. Ibid., **14**(4): 645–649.

1957c. Alterations in the blood level of lactic acid in certain salmonid fishes following muscular activity. III. Sockeye salmon, *Oncorhynchus nerka*. Ibid., **14**(6): 807–814.

1958. Hyperactivity as a lethal factor in fish. Ibid., **15**(4): 573–586.

BLACK, E. C., A. R. CONNOR, K. LAM, AND W. CHIU. 1962. Changes in glycogen, pyruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. Ibid., **19**: 409–436.

BLACK, E. C., A. C. ROBERTSON, A. R. HANSLIP, AND W. C. CHIU. 1960. Alterations in glycogen, glucose and lactate in rainbow and Kamloops trout, *Salmo gairdneri*, following muscular activity. Ibid., **17**(4): 487–500.

BLACK, E. C., A. C. ROBERTSON, AND R. R. PARKER. 1961. Some aspects of carbohydrate metabolism in fish. *In* A. W. Martin [ed.] Comparative physiology of carbohydrate metabolism in heterothermic animals. Univ. Wash. Press, Seattle, Wash. p. 89–124.

BLAZKA, P., M. VOLF, AND M. CEPELA. 1960. A new type of respirometer for the determination of metabolism of fish in an active state. Physiol. Bohemoslov., **9**: 553–558.

CAILLOUET, C. W., JR. 1964. Blood lactic acid concentration of unexercised and exercised mature carp in winter and summer. Iowa State J. Sci., **38**(3): 309–322.
1967. Hyperactivity, blood lactic acid and mortality in channel catfish. Iowa State Univ. Sci. Tech. Res. Bull., **551**: 897–915.

CARROLL, N. V., R. W. LONGLEY, AND J. H. ROE. 1956. The determination of glycogen in liver and muscle by use of anthrone reagent. J. Biol. Chem., **220**: 583–593.

FRASER, D. I., E. LO, AND W. J. DYER. 1966. Nucleotide interference with glycogen estimation in white and red muscle of cod. J. Fish. Res. Bd. Canada, **23**(6): 921–924.

HAMMOND, B. R., AND C. P. HICKMAN, JR. 1966. The effect of physical conditioning on the metabolism of lactate, phosphate and glucose in rainbow trout, *Salmo gairdneri*. Ibid., **23**(1): 65–83.

HAWK, P. B., B. L. OSER, AND W. H. SUMMERSON. 1947. Practical physiological chemistry, 12th ed. The Blakiston Company, Philadelphia, Pa.

HEATH, A. G., AND A. W. PRITCHARD. 1962. Changes in the metabolic rate and blood lactic acid of bluegill sunfish, *Lepomis macrochirus*, Raf., following severe muscular activity. Physiol. Zool., **35**(4): 323–329.

MONTGOMERY, R. 1957. The determination of glycogen. Arch. Biochem. Biophys., **67**: 378–386.

MUIR, B. S., G. J. NELSON, AND K. W. BRIDRES. 1965. A method for measuring swimming speed in oxygen consumption studies on the aholehole, *Kuhlia sandvicensis*. Trans. Am. Fish. Soc., **94**(4): 378–382.

NAKATANI, R. E. 1957. Changes in the inorganic phosphate and lactate levels in blood plasma and muscle tissue of adult steelhead trout after strenuous swimming. Univ. Wash. School Fish. Tech. Rept. No. 30. 14 p.

PARKER, R. R., AND E. C. BLACK. 1959. Muscular fatigue and mortality in troll-caught chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Bd. Canada, **16**(1): 95–106.

PARKER, R. R., E. C. BLACK, AND P. A. LARKIN. 1959. Fatigue and mortality in troll-caught Pacific salmon (*Oncorhynchus*). Ibid., **16**(4): 429–448.

SNEDECOR, G. W. 1948. Statistical methods. 4th ed. Iowa State College Press, Ames, Iowa. 485 p.

STANLEY, J. 1960. Lucid biometrics. 1st ed. McGill Univ. Bookstore, Montreal, Que. 99 p.

STEEL, G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York. 481 p.

WENDT, C. 1965. Liver and muscle glycogen and blood lactate in hatchery-reared *Salmo salar* L. following exercise in winter and summer. Rept. Inst. Freshwater Res., Drottningholm, **46**: 167–184.

Glucose Metabolism in the Caecum of the Marine Borer *Bankia setacea*[1]

By D. Liu and P. M. Townsley[2]

British Columbia Research Council
University of British Columbia Campus, Vancouver, B.C.

ABSTRACT

The degradation of uniformly labelled glucose-C^{14} was followed in the caeca preparations of the marine wood borer *Bankia setacea* (Tryon). This digestive organ was found to contain large quantities of soluble protein. Various accumulating intermediates were isolated, indicating the presence of enzymes typical of the Embden–Meyerhof pathway, the pentose pathway, the citric acid cycle, and the non-triose pathway. The presence of wood in the caeca may be required for the synthesis of glutamic and aspartic acids within the caeca. Approximately 10% of the added glucose was found in an unidentified, unstable, electronegative compound called glucose-X. The function of this compound is unknown.

INTRODUCTION

The marine borer is a bivalve member of the mollusc family. The valves of this mollusc have a file-like surface which are used to rasp into floating logs and unprotected wooden marine structures. Once the larvae of the borer have established themselves on a desirable wooden surface, growth and the resultant destruction of wooden structures can be very rapid. All of the wood obtained by the rasping action of the shell passes into the alimentary tract via a short oesophagus. Leaving the oesophagus of the adult, the wood chips enter a tube-like stomach into which connect the ducts of several small distinct "livers" or "digestive glands." Histological examination of the posterior liver reveals that it is divided into two functional regions suggestive of a digestive area and an excretory area with a common ciliated duct into the stomach. Large numbers of wood chips ascend into the posterior liver duct and are readily observed within the lumen. Large free phagocytic cells, possibly arising from the phagocytic walls of the digestive area, roam the lumen throughout the liver engulfing wood raspings. The occurrence of these free phagocytic cells is a characteristic of the marine borer and is probably related to the ability of the borer to digest large quantities of wood and to grow very rapidly. Unlike the digestive area, the cell walls of the excretory area of the liver have yellow-colored inclusions and do not possess phagocytic cells, although free phagocytic cells are found in the lumen (Potts, 1923).

At least a portion of the ingested particles of wood leave the stomach and enter the caecum which is a very large, long-blind, thin-walled tube opening

[1]Received for publication October 30, 1967.
[2]Present address (P.M.T.): Faculty of Agriculture, University of British Columbia, Vancouver 8, B.C.

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at the anterior end. The ventral wall of the caecum is enfolded throughout its length forming a typhlosole which is supplied with a large artery. When the shipworm is boring, the caecum is always full of wood filings and it would appear that this organ is probably the primary location in which the wood is digested. The so-called digestive area of the posterior liver is insignificant in terms of size in comparison with the caecum.

The enzymes, e.g. cellulase and cellobiase, that are required to reduce the wood chips within the stomach–liver area and within the caecum into component glucose subunits have been demonstrated (Greenfield and Lane, 1953; Boynton and Miller, 1927). The function of the phagocytic cells or of the digestive area of the liver cannot be explained in the light of the function of the large digestive area of the caecum.

The purpose of this investigation is to provide additional knowledge as to the function of the caecum by determining the fate of glucose released by the enzymes of cellulose degradation.

MATERIALS AND METHODS

Actively boring healthy marine borers, ranging from 6 to 12 inches long, were removed from logs maintained in local marine waters. The animals were dissected and the posterior end of the caecum, approximately 1 inch long (Fig. 1), was cut off and immediately used in the experiments. Care was taken to avoid including gonadal tissues. Three different tissue preparations were used to help elucidate the function of the caecum. First, a microsyringe containing 10 μliters of glucose-C^{14} was inserted into the center of the cut end of the caecum and the radioactive glucose deposited into the caecal contents throughout the entire length of the caecum. Second, caecum supernatant was prepared by expressing the posterior portion of the caecum in a very loose-fitting Potter homogenizer followed by centrifugation at 7000 × *g* for 15 min. Third, caecum contents naturally depleted of all wood chips "endogenous" were obtained by removing healthy active marine borers from wood which had recently become depleted by tremendous borer activity and the clear light-yellow aqueous caecal fluid was drained through a small puncture in the caecum wall. All of the animals contained visibly large amounts of glycogen in the mantle tissues.

The caeca preparations were incubated at a constant temperature of 20 C for a period of 4 hr, and then either crushed in a loose-fitting Potter homogenizer, or simply mixed at 0 C, in an equal volume of 2 N perchloric acid and centrifuged. The supernatant was neutralized with potassium hydroxide and the potassium perchlorate removed by centrifugation. The supernatant was concentrated with a jet of dry air,[3] streaked on Whatman #3-mm chromatogram paper, and fractionated by electrophoresis[4] in 0.1 M triethylamine–acetic acid buffer at *p*H 8.4 for 4–6 hr at 300 v difference of potential at the electrodes with a current of 10 ma. The radioactive fractions were located by autoradiography using Kodak Medical X-ray, royal blue

[3]Due to evaporation, the sample remained near freezing during the drying period.
[4]Research Equipment Corporation, Oakland, California, Model E-800-2.

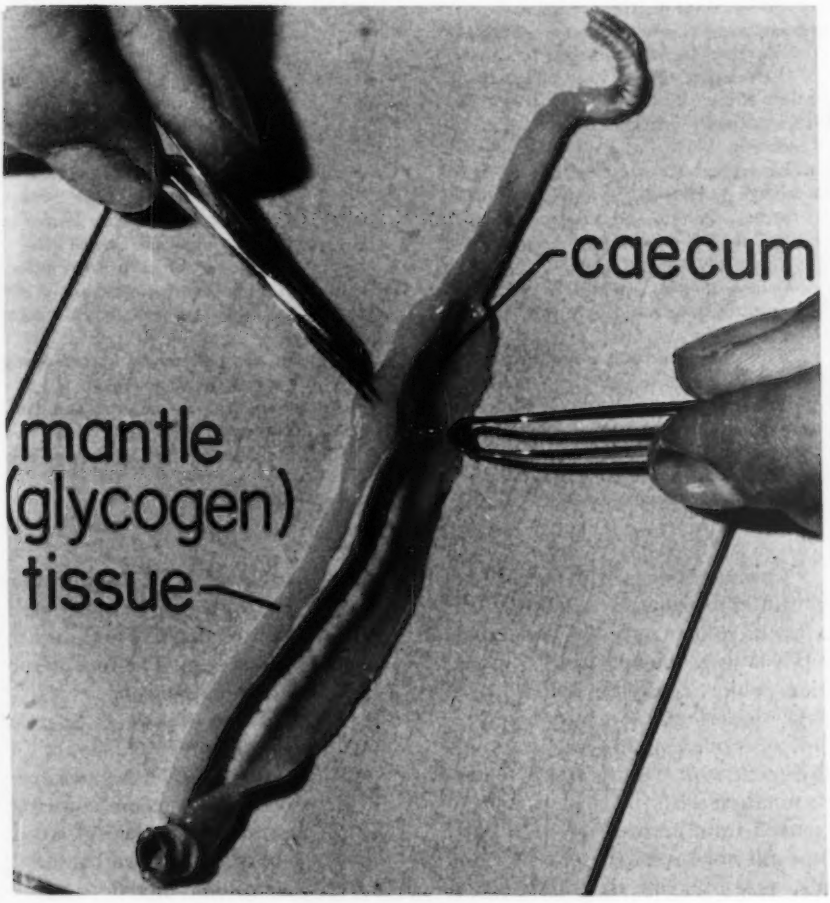

FIG. 1. Exposed caecum of the marine borer *Bankia setacea* (Tryon).

film, or by scanning the electrophoresis paper strip with a Nuclear Chicago Actigraph III. Direct visual location of the intermediates and compounds of interest were detected by the reagents described in the text. The radioactive components were eluted out of each band and applied to Whatman #4 paper for chromatography. Several different solvents along with co-chromatography with known compounds were used to identify every compound.

Solvents for chromatography (Smith, 1960; Block et al., 1955) were: ethyl acetate:acetic acid:water (3:1:3 v/v) EtAc; isopropanol:formic acid:water (75:12.5:12.5) IsoFm; ethanol: ammonia:water (180:10:10) EtAm[1]; pyridine:*n*-butanol:water (60:60:60) PyBu; pyridine:ethyl acetate:water (25:60:20) PyAc; phenol:water (80:20) ph; *n*-butanol:acetic acid:water (120:30:50) BuAc; ethanol:ammonia:water (160:10:30) EtAm[2]; cellusolve:ammonia:water (80:5:15) CeAm.

Solvents for electrophoresis were: 0.1 M triethylamine–acetic acid buffer *p*H 8.4. E+Am; pyridine:acetic acid:acetone:water (1.5:5.5:15:78) E+Py.

Enzyme: bacterial alkaline phosphatase, Pase.

Developing agents: (*a*) carbohydrates: alkaline silver nitrate (Smith, 1960); periodate alkaline silver nitrate (Whistler and Wolfram, 1962); aniline–diphenylamine reagent (Smith, 1960); periodate–benzidine reagent (Smith, 1960); (*b*) amino acids: ninhydrin-2, 4, 6-collidine (Randerath, 1963); (*c*) acids and phosphorylated compounds: aniline–xylose (Smith, 1960); acridine reagent (Smith, 1960). This method has been modified by us in order to increase its sensitivity. Acridine (0.1 g) is dissolved in 100 ml of acetone. The chromatogram is drawn through the reagent, drained, and hung in a fume hood for 3 min. The chromatogram is then heated to 90–100 C for 2–3 min. The acids appear as yellow spots when viewed under ultraviolet light.

Uniformly labelled glucose-C^{14}, 196 mc/mM, supplied by Nuclear Chicago Corporation, Des Plaines, Illinois, was purified before use in the experiments by paper electrophoresis at *p*H 8.4 as described, followed by paper chromatography using the solvent ethyl acetate:acetic acid: water (3:1:3 v/v).

Free glucose present in the caecum after deproteinization was determined by enzymatic oxidation with glucose oxidase (Glucostat, Worthington Biochemical Corp., Freehold, N.J.).

Protein was measured by the biuret reaction (Layne, 1957) with egg albumin as a standard. Measurement of the protein concentration by direct optical density readings or reactions based on the presence of aromatic amino acids was not possible due, in part, to the high soluble lignin content of the caecal preparations.

Dry weight was determined by drying the sample under vacuum at 80 C for 16 hr.

RESULTS

Caecum tissues with included wood chips from active boring shipworms contain approximately 21% dry matter of which one third can be attributed to water soluble protein as determined by the biuret reaction. Free glucose in this matrix amounts to 19.5 mg/g dry weight of the caecum. The free amino acids, which could be readily detected by paper chromatography of 80% ethyl alcohol extracts or perchloric acid extracts of caecum were aspartic acid, glutamic acid, glycine, taurine, β-alanine, and alanine which are in agreement with the investigations of Drisko and Hochman (1957). Microscopic examination with phase contrast at 980 magnification of the caecum contents removed from marine borers full of wood chips or completely devoid of wood chips did not reveal the presence of any microflora above one or two bacterial cells, possibly contaminates, introduced during isolation. Microflora were observed in caeca removed from marine borers in rotting wood or from diseased areas. However, the identity of microflora in the caecum under various circumstances was rarely the same and, as a result, would indicate that the microflora had little, if any, essential part in the digestion and metabolism of wood.

Uniformly labelled glucose is metabolized by the "intact" caecum into a number of intermediates characteristic of the Embden–Meyerhof pathway, of the pentose pathway, of the citric acid cycle (TCA cycle), and of the non-triose phosphate pathway as shown in Table I. From an estimated relative 210,000 counts/min added as glucose-C^{14} into the caeca, contents of excised caeca, 132,114 counts/min, were isolated in the supernatant without washing of the pellet and applied to 3-mm filter paper for fractionation by electrophoresis at *p*H 8.4 (Fig. 2). Except for three unknown neutral compounds, all of the

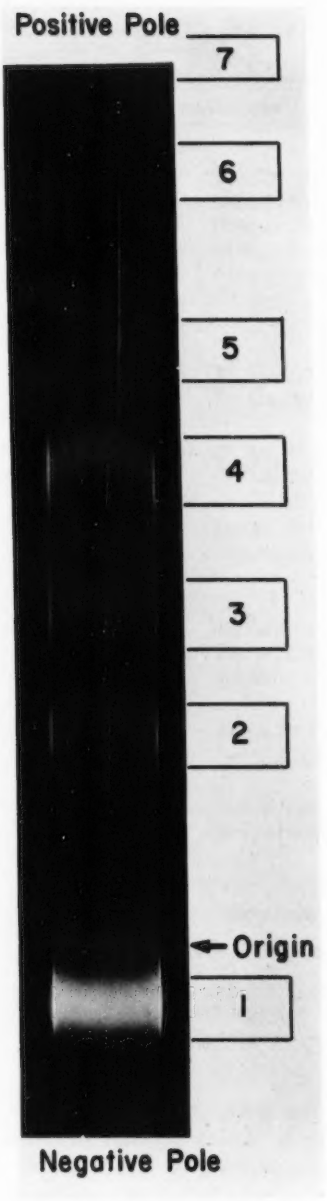

FIG. 2. The electrophoretic separation of C^{14} labelled compounds found in the caecum after 4 hr incubation of glucose-C^{14} at 20 C after injection into the contents of the caecum.

TABLE I. Carbon labelled compounds found in the caecum[a] after injection of uniformly labelled glucose-C^{14}.

Electrophoresis band[b]	Total count/min of each band[c]	Intermediate identified		
		Compound	Counts/min[d]	Solvent system
I	69,468	Glucose	33,225	EtAc;IsoFm; E+Am
		Fructose	748	EtAc;IsoFm; E+Am
		Cellobiose	7,503	EtAc;IsoFm; E+Am
		Alanine	17,871	EtAc;IsoFm; EtAm[1];PyBu
		Unknown #1	2,357	
		Unknown #2	3,472	
		Unknown #3	1,361	
II	13,818	Gluconic	676	E+Am;PyAc;IsoFm;EtAm;BuAc
		Glucose-X	9,954	E+Am;PyAc;IsoFm;EtAc
		Unknown	None	
III	11,358	Glutamic	6,893	E+Am;PyAc;IsoFm; Ph
		Aspartic	1,387	E+Am;PyAc;IsoFm; Ph
		Unknown	None	
IV	17,478	Lactic	11,370	IsoFm;E+Py
		Glucose-6-P	195	IsoFm;EtAc;E+Am
		Unknown	None	
V	3,438	Fructose-1		
		6-diP	1,101	IsoFm;E+Py;EtAc(Pase)
		Glycerol-P	301	IsoFm;BuAc;PyAc(Pase);Et Ac(Pase)
		Ribose-X-P	60	E+Am;EtAc(Pase)
		Unknown	None	
VI	4,176	Malic	1,537	IsoFm;E+Py;EtAm[2];CeAm
		Succinic	2,489	IsoFm;EtAm[2];BuAc(Pase);E+Py(Pase)
		Unknown	None	
VII[e]	648	Iso-citric	256	IsoFm;BuAc;E+Am
		Citric	264	IsoFm;BuAc;E+Am
		Unknown	None	

[a]Experiment contained six caeca, total wet weight approximately 1.5 g.
[b]Electrophoresis band as indicated in Fig. 2.
[c]Total counts/min present of each individual band before extraction of the band from the electrophoresis strip.
[d]Total counts/min isolated and identified as a particular compound.
[e]Total counts/min present in the $HClO^4$ extract added to the electrophoresis strip, as measured by Actigraph III, was 132,114.

compounds which contained sufficient radiation to permit tracing during isolation were characterized. The relative values of the disintegrations listed for the intermediates are an indication of the relative amount of the isotope accumulation in the intermediate. Both radioactive alanine and lactic acid accumulate very rapidly. Lactic acid is shown in Fig. 2, band 4. It is interesting to note that the compound pyruvate, parent of alanine and lactic acid, was not detected.

Approximately 10% of the total radiation added in terms of glucose occurred in an electronegative, unstable compound, which we have called for convenience glucose-X. The formation of glucose-X would appear to be non-enzymatic in that it could be produced in caecal preparations which had been heated to a temperature of 80 C for 4 min. The compound was unstable to dry storage at room temperature on chromatograph paper and to chromatography in strongly acid or basic solvents. Glucose-X decomposed to free glucose and to an unknown compound or compounds which are presently under study. Cellobiose was noted occasionally to exhibit an electronegative character on electrophoresis and it is possible that a similar complex to glucose-X also occurs with cellobiose. Glucose-X does not appear to be composed of a conjugate with the phenolics found in wood (Dutton, 1966).

The endogenous caeca preparation (Table II) degraded glucose to the intermediates lactic acid and alanine, indicating the presence of the Embden–

TABLE II. Carbon labelled compounds found in endogenous preparations of caeca after the addition of uniformly labelled glucose-C^{14}.

Electrophoresis band[a]	Metabolic intermediate	Endogenous caeca[b] (*counts/min*)
I	Glucose	31,633
	Fructose	N.D.[c]
	Cellobiose	289
	Alanine	331
	Ribose	N.D.
II	Gluconate	605
	Glucose-X	230
	Cellobiose	N.D.
III	Glutamic acid	N.D.
	Aspartic acid	N.D.
	Unknown acid	319
	Unknown ninhydrin compound	N.D.
IV	Lactic acid	710
	Glucose 6-P	N.D.
V	Fructose 1, 6-diP	N.D.
	Glycerol-P	N.D.
	Ribose X-P	N.D.
VI	Malic acid	N.D.
	Succinic acid	80
VII	Isocitric acid	N.D.
	Citric acid	N.D.

[a]Electrophoresis band as indicated in Fig. 2.
[b]Four caeca were used in the experiment.
[c]Not detectable.

Meyerhof glycolytic pathway shown to occur in whole caeca (Table I). However, there were a few notable differences between the results given by the two latter preparations. In the experiment using endogenous medium, the accumulating degradation products of glucose-C^{14} were not found to occur in as high a concentration per caecum as in the experiments using intact caeca. The labelled aspartic and glutamic acids, as well as the non-labelled amino acids, could not be detected and in their place, travelling in the same location in the electrophoresis paper, was an unknown acid whose behaviour on chromatography in three solvent systems closely resembled α-ketoglutarate. The true identity of this acid compound is still in question. A small amount of succinic acid was found in the endogenous preparation but no other member of the TCA cycle accumulated. Glucose-X occurred in low concentration.

In Table III there is reported the data on two experiments, supernatant and intact caeca, from marine borers removed from a sample of wood at the same time to avoid the possible effects of seasonal variation on metabolism.

TABLE III. Carbon labelled compounds found in supernatant preparations of caeca after the addition of uniformly labelled glucose-C^{14}.

Electrophoresis band	Metabolic intermediate	Supernatant 1 Caecum (1 μc)[a] (*counts/min*)	Intact caecum 1 Caecum (0.5 μc)[a] (*counts/min*)
I	Glucose	57,001	4,199
	Fructose	601	N.D.[b]
	Cellobiose	1,904	434
	Alanine	N.D.	1,083
	Ribose	153	N.D.
II	Gluconate	571	N.D.
	Glucose-X	17,043	2,786
	Cellobiose	524	N.D.
III	Glutamic acid	356	439
	Aspartic	79	72
	Unknown acid	N.D.	N.D.
	Unknown ninhydrin compound	N.D.	N.D.
IV	Lactic acid	957	1,488
	Glucose 6-P	N.D.	Not identified
V	Fructose, 1,6-diP	N.D.	" "
	Fructose 1,6-diP	N.D.	" "
	Glycerol-P	N.D.	" "
	Ribose X-P	N.D.	" "
VI	Malic acid	N.D.	229
	Succinic acid	N.D.	655
VII	Isocitric acid	N.D.	N.D.
	Citric acid	N.D.	N.D.

[a]Amount of isotope initially added.
[b]Not detectable.

Primarily, the experiment was designed to locate the presence of glucose-X in the supernatant. However, other intermediates of glucose metabolism were determined to complete the analysis. It is not recommended that the small differences in the counts per minute of the isolated products of glucose degradation be considered significant. However, the differences borne out by the absence of succinate and of alanine in the caeca 7000 × *g* supernatant would appear to be real.

DISCUSSION

Microscopic examination of the caecal contents did not reveal the presence of microorganisms in sufficient numbers or of constant microbial identification to account for the metabolic products observed. On occasion, a bacterial or a protozoan population was detected but this was thought to be associated with adverse environmental conditions or with dying marine borers. On the other hand, the livers with their large ducts into the stomach would appear to be the logical source of the digestive enzymes found in the caecum. The function of the liver phagocytic cells containing wood chips cannot be explained satisfactorily in the light of the suggested function of the caecum. Whether or not all of the enzymes present in the caecum are derived from one excretory liver tissue or lysis of cells or whether each of the various livers has a responsibility for providing an enzyme system remains an interesting question.

The presence of the high concentration of free glucose and soluble protein within the caecum would appear to supply sufficient osmotic pressure to offset the salinity of the ocean water, which is in direct contact with the caecum via the infrabranchial cavity. However, qualitative paper chromatographic examination of the free amino acids reveals the presence of considerable amounts of taurine, an amino acid found in marine molluscs but not in closely related freshwater molluscs. The function of taurine has been stated as an osmotic regulator (Simpson et al., 1959). It is interesting to note that the amino acid β-alanine also appeared in an apparently high concentration in free form. Both these amino acids do not become labelled with the carbon from uniformly labelled glucose within the 4-hr duration of the experiment.

An alternative explanation for the presence of taurine could be that β-alanine and taurine may be associated with co-enzyme A or an acyl carrier protein as the components β-alanine and mercaptoethylamine (Sauer et al., 1964). Co-enzyme A would presumably be required for the synthesis of the fatty material known to accumulate[5] in the cells of the marine borer. Preliminary experiments indicated that the addition of mercaptoethylamine into the contents of excised caeca did not increase visibly the taurine content on solution and detection by ninhydrin when compared with controls. Mercaptoethylamine was, however, quickly altered to several unidentified compounds during the incubation period.

[5]Unpublished data of observations on *Bankia setacea* tissue in tissue culture.

Glucose was degraded rapidly to lactic acid by the contents of the caecum. The enzymes necessary for these reactions were found in the supernatant after centrifugation of the caecal content containing wood chips at 7000 × *g* for 15 min and in the uncentrifuged clear caecal fluid removed from marine borers which have exhausted their wood supply. The accumulation of lactic acid was increased if the glucose was injected into the caecum in comparison with the addition of glucose to removed caecal contents, to centrifuged caecal supernatants, or to endogenous caecal fluids. Presumably, the formation of lactic acid in the intact organ is favored possibly due to the increased anaerobiosis.

An evaluation of the relative contribution of the pentose cycle and of the Embden–Meyerhof glycolytic pathway in the degradation of glucose cannot be answered with the present data. Undoubtedly both pathways are present in the intact caecal preparations and, very likely, the relative contribution of each pathway is seasonal, favoring pentose formation during rapid gonadal development. What controls the contribution of these two pathways presents an interesting question. The pentose cycle is not considered to be an important energy-yielding route, but more likely a means of obtaining a number of carbon compounds required by the organism and to supply a source of reduced nicotinamide adenine dinucleotide phosphate. The gonadal tissues almost completely incase the caecum throughout its length, theoretically enabling the products of the pentose cycle to be readily available for the synthesis of genetic material.

The tricarboxylic acid cycle intermediates accumulate and can be detected within the 4-hr incubation period of glucose-C^{14} injected excised caeca. The electron transport chain and the system for the production of adenosinetriphosphate through oxidative phosphorylation are believed generally to be located in the mitochondria. Similarly, the intact TCA cycle also operates within the mitochondria to provide the carbon skeletons to meet cell requirements.

Thus it would appear from these studies that all of the enzymes for the digestion of wood, and the degradation of the resulting glucose molecules, reside in the caecum. The presence of a glycolytic pathway degrading glucose to lactic acid and a pentose cycle most certainly exists within the caeca contents. The presence of accumulating intermediates typical of the TCA cycle can be easily detected in "intact" caeca and only with difficulty, with the exception of the intermediate succinate, in the soluble contents of the caeca.

Aspartic acid and glutamic acid can be found in centrifuged supernatant caecum extracts, which would suggest the occurrence of the corresponding ketoacids, oxalacetic and α-ketoglutaric acid. On the other hand, it is tempting to postulate that the complete absence of the soluble amino acids aspartic and glutamic acid in the endogenous caeca preparations would indicate a dependence on the metabolism of wood for these two amino acids. The absence of these two amino acids in the endogenous preparations may also explain, in part at least, the frequent field observation in depleted logs of dead marine

borers still containing large amounts of mantle glycogen tissue. The present data cannot substantiate the latter postulation but it does point to a very interesting question of amino acid synthesis in the absence of wood.

The detection of succinate among the labelled compounds accumulating in the endogenous caecal liquid may support the possibility that the pathway of glucose degradation in the wood boring mollusc resembles that described by Simpson and Awapara (1966) for the mantle tissues of several marine molluscs, an example being the oyster. The latter authors found that the succinic acid and small amounts of lactic acid were the major organic acids found in glucose degradation and thus proposed the carboxylation of phosphoenolphruvate to oxalacetate. Oxalacetate was converted to succinate via malate and fumarate.

Alanine is absent in the degradation products of glucose-C^{14} in the reaction medium containing 7000 $\times$ g caecal supernatant. On the other hand, the presence of alanine in both the injected intact caeca and in the endogenous caeca solution would indicate that the mechanism of amination or transamination has been lost, probably adsorbed and carried down with the centrifuged pellet of caeca sawdust.

ACKNOWLEDGMENTS

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REFERENCES

Block, R. J., E. L. Durrum, and G. Zweig. 1955. A manual of paper chromatography and paper electrophoresis. Academic Press, Inc., New York, N.Y.

Boynton, L. C., and R. C. Miller. 1927. The occurrences of a cellulase in the shipworm. J. Biol. Chem., **75**: 613–618.

Drisko, R. W., and H. Hochman. 1957. Amino acid content of marine borer. Biol. Bull., **112**: 325–329.

Dutton, D. J. 1966. Uridine diphosphate glucose and the synthesis of phenolic glucosides by mollusks. Arch. Biochem. Biophys., **116**: 399–405.

Greenfield, L. J., and C. E. Lane. 1953. Cellulose digestion in *Teredo*. J. Biol. Chem., **204**: 669–672.

Layne, E. 1957. Spectrophotometric and turbidimetric methods for measuring proteins. *In* S. P. Colowick and N. O. Kaplan [ed.] Methods of enzymology, Vol. 3. Academic Press, Inc., New York, N.Y. p. 450.

Potts, F. A. 1923. The structure and function of the liver of *Teredo* the shipworm. Proc. Cambridge Phil. Soc. (Biol. Sci.), **1**: 1–17.

Randerath, K. 1963. Thin-layer chromatography. Academic Press, Inc., New York, N.Y. 94 p.

Sauer, F., E. L. Pugh, S. J. Wakil, R. Delaney, and R. L. Hill. 1964. 2-Mercaptoethylamine and β alanine as components of acyl carrier protein. Proc. Natl. Acad. Sci., **52**: 1360–1366.

Simpson, J. W., K. Allen, and J. Awapara. 1959. Free amino acids in some aquatic invertebrates. Biol. Bull., **117**: 371–381.

Simpson, J. S., and J. Awapara. 1966. The pathway of glucose degradation in some invertebrates. Comp. Biochem. Physiol., **18**: 537–548.

Smith, I. 1960. Chromatographic and electrophoretic techniques, Vol. 1. Interscience Publishers, Inc., New York, N.Y.

Whistler, R. L., and M. L. Wolfrom [ed.]. 1962. Methods in carbohydrate chemistry. Vol. 1. Academic Press, Inc., New York, N.Y.

Ultrastructure of Trout Cornea[1]

By Henry F. Edelhauser and Kenneth A. Siegesmund

Department of Physiology, Ophthalmology and Anatomy
Marquette School of Medicine, Milwaukee, Wisc., U.S.A.

ABSTRACT

The ultrastructure of the brook, brown, and rainbow trout cornea as observed using the light and electron microscopes is described. The transition between the central and limbal areas of the cornea is included. The limbal region, unlike the central cornea, contained epithelial microvilli, unorganized Bowman's membrane with various size collagen fibrils, and a stroma containing melanocytes and capillaries. These corneas also possess prominent keratocytes and an endothelium.

INTRODUCTION

In the past decade there has been extensive research in the state of Michigan concerning the eye disease that occurs in hatchery-reared lake trout. Allison (1963) reported that hatchery lake trout developed cataracts which resulted in permanent damage to the eye. Further studies by Hoffert and Fromm (1965) showed that these hatchery-reared lake trout also develop corneal lesions, which occur in a progression of four stages leading eventually to corneal perforation, extrusion of the lens, and blindness. Edelhauser et al. (1966) showed that the epithelium of the cornea in the diseased trout is impermeable to water and that corneal edema associated with the disease is of endothelial origin. These trout corneas are also impermeable to sodium ion despite the presence of an osmotic gradient favoring the movement of sodium out of the cornea (Edelhauser et al., 1968). Sodium ions have recently been localized in the trout cornea by means of an electron-dense precipitate of sodium pyroantimonate by Edelhauser and Siegesmund (1968). It was evident from this localization that the barrier to sodium movement across the teleost cornea is located in the basal cell layer of the epithelium.

Because of all the interest in the trout cornea (both normal and pathological), the purpose of this paper is to describe its ultrastructure.

MATERIALS AND METHODS

The corneas of seven brown trout (*Salmo trutta*), eight rainbow trout (*Salmo gairdneri*), and four brook trout (*Salvelinus fontinalis*) were removed from the eye and each placed in a drop of fixative on a slab of wax. Small "pie-shaped" wedges were cut from the center of the cornea and fixation continued for 1½ hr. The tissue was rinsed briefly in distilled water, rapidly dehydrated in graded acetone solutions, and embedded in Vestopal W

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(Martin Jaeger, 1222 Vesenaz, Geneve, Switzerland). Sections were cut on a Porter-Blum microtome, stained in uranyl acetate and lead citrate, and examined in an RCA-EMU 3b electron microscope.

The fixative consisted of 2% acrolein and 1–1½% glutaraldehyde buffered at a *p*H of 7.2 with phosphate. Fixation in this solution was for 30 min followed by 1 hr of fixation in 2% osmic acid buffered at *p*H 7.3 with veronal acetate.

OBSERVATIONS

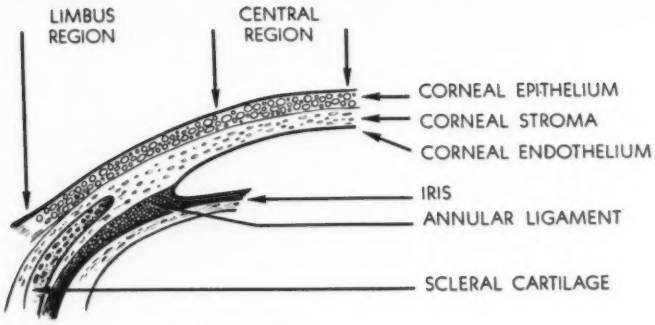
A diagram (Fig. 1) of a sagittal section of the trout cornea illustrates the limbus and central region. A cross-section of the central trout cornea examined under the light microscope (Fig. 2) illustrates the various cells and layers of the cornea. The total thickness of the central cornea was found to be 0.15–0.25 mm with 40% of the total consisting of epithelium and 12.5% of the remaining thickness made up of Bowman's membrane. Corneas of all three species were observed to have similar structure.

Cells in the outer layer of the central corneal epithelium (Fig. 3) are squamous and those in direct contact with the environmental water are continually sloughed off; therefore, they appear less dense than the cells immediately below them. The desmosomes, or attachment bodies, resemble black sutures holding the cells together. The epithelial cells show two distinct areas of cytoplasm: a dense outer area composed of tonofibrils and a less dense inner area containing mitochondria and endoplasmic reticulum. Toward the limbus (Fig. 4), the surface becomes increasingly irregular and the epithelial cells possess microvilli. The cytoplasm of these outer epithelial cells contains secretory droplets and a prominent Golgi body.

The basal epithelial cells of the central cornea are more nearly columnar in shape and rest upon a thin electron-dense basement membrane (Fig. 5). The basal lamina is structurally similar to that found in human (Jakus, 1964) and dogfish cornea (Goldman and Benedek, 1967). The basement membrane and basal lamina also appear to interdigitate into the basal epithelial cells. The lamina ends at the termination of the electron-dense material, where the underlying Bowman's layer begins.

One of the apparent changes observed in sections of the cornea near the limbus (Fig. 6) is a change in the basal epithelial cells from a columnar type to a more cuboidal type. Also, the demarcation of two distinct areas of cytoplasm, as in central epithelial cells, is lost. The electron density of the basement membrane and basal lamina is less than in the central cornea (Fig. 5). Bowman's layer changes markedly as it approaches the limbus, becoming thinner and more loosely packed (Fig. 6). The collagen fibrils are of various sizes and an amorphous material can be observed between them.

The collagen fiber feltwork of Bowman's layer (Fig. 7) appears to have some degree of orientation, becoming specifically orientated into collagen lamellae of layers (Fig. 8) in the remainder of the stroma. In any field of a section cut from a suitably oriented block, fibrils of one lamella form essentially right angles with those in adjacent layers.



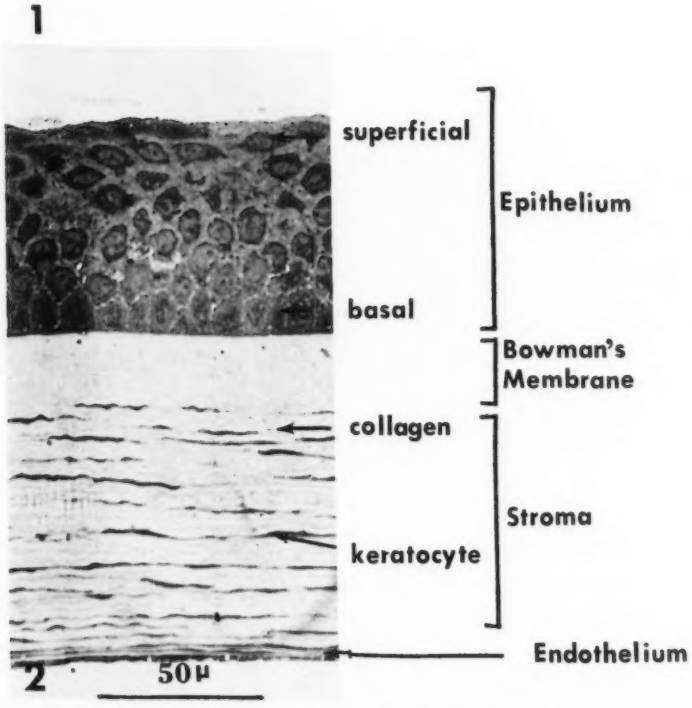


FIG. 1. Diagram of a sagittal section of the trout cornea.

FIG. 2. Photomicrograph of trout cornea showing superficial and basal epithelial cells, Bowman's membrane, stroma comprised of collagen and keratocytes, and endothelium. This 0.5-μ thick section was cut from the same block used to obtain the electron micrographs. The section was stained with toluidine blue. ×510.

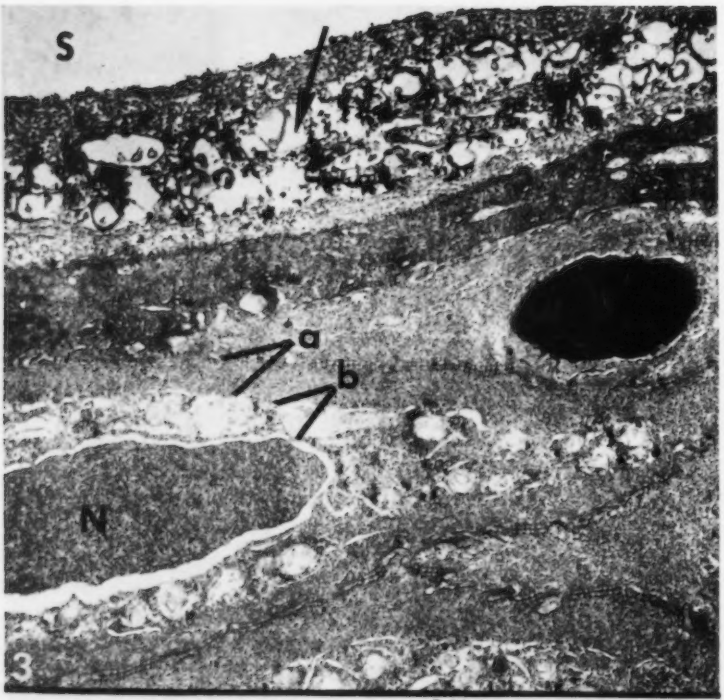


FIG. 3. The outer layer of epithelial cells from the central cornea. The arrow indicates an outer epithelial cell which is in the process of being sloughed off. "S" indicates surface of epithelium exposed to environmental water. Deeper epithelial cells possess a nucleus (N) and distinct areas of cytoplasm, a dense outer area (*a*) and a less dense inner area of cytoplasm (*b*). ×11,000.

FIG. 4. Limbal region of the cornea possesses superficial epithelium with microvilli (MV). ×11,500. The insert at the left is also limbal corneal epithelium, demonstrating secretory droplets (arrow) and a prominent Golgi body (G). ×8000.

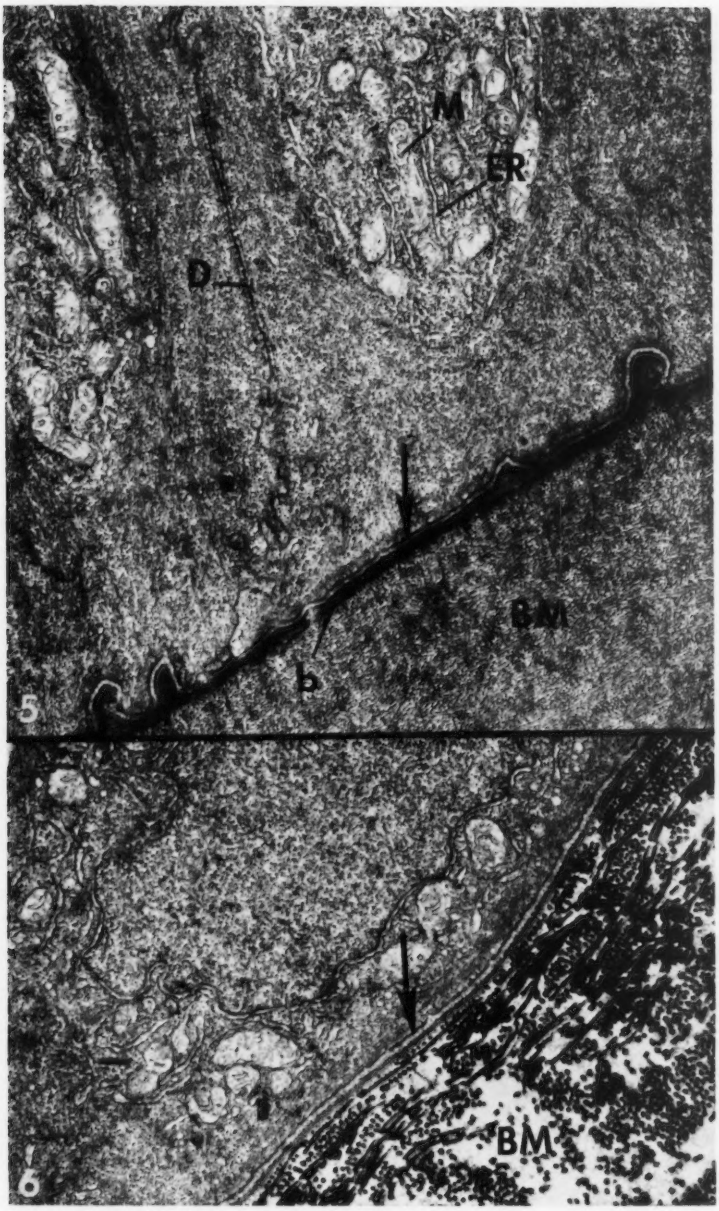


FIG. 5. Basal epithelial cells of the central cornea showing cytoplasmic organelles such as mitochondria (M) and endoplasmic reticulum (ER). These columnar-shaped cells show desmosomes (D) between adjacent cells and rest upon a thin, electron-dense basement membrane (arrow). The basal lamina (*b*) and Bowman's membrane (BM) underlie the basal epithelial cells. ×14,000.

FIG. 6. A basal epithelial cell in the peripheral cornea, the basement membrane (arrow), and Bowman's membrane (BM). ×14,000.

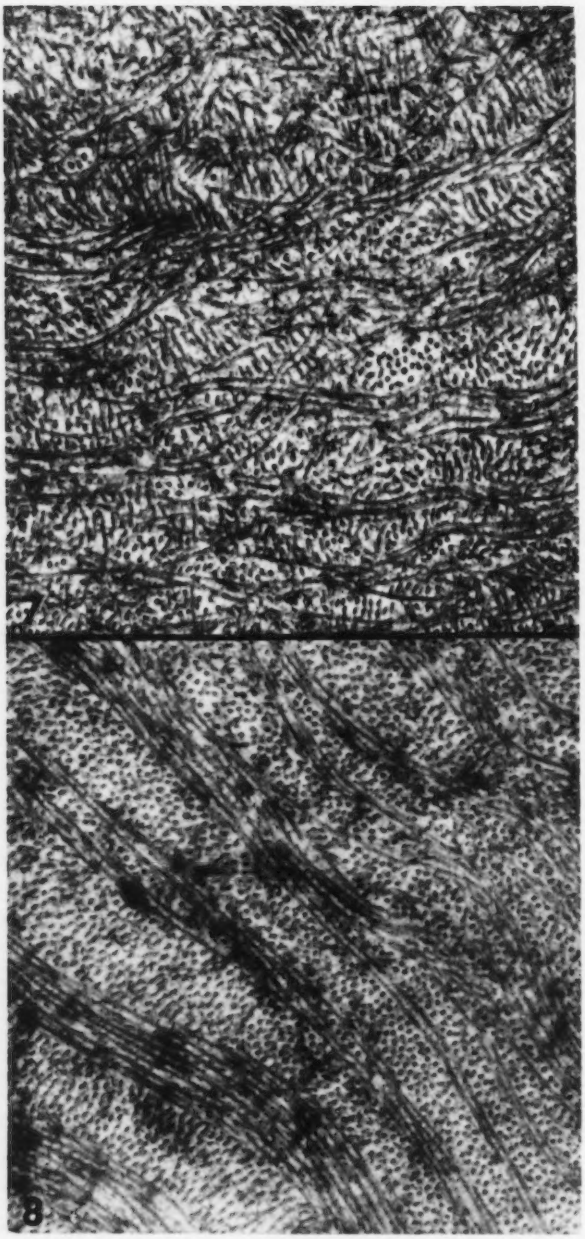


FIG. 7. The collagen of Bowman's layer in the central cornea directly beneath the basal lamina. ×33,500.

FIG. 8. Stroma collagen showing organized lamellae. ×46,000.

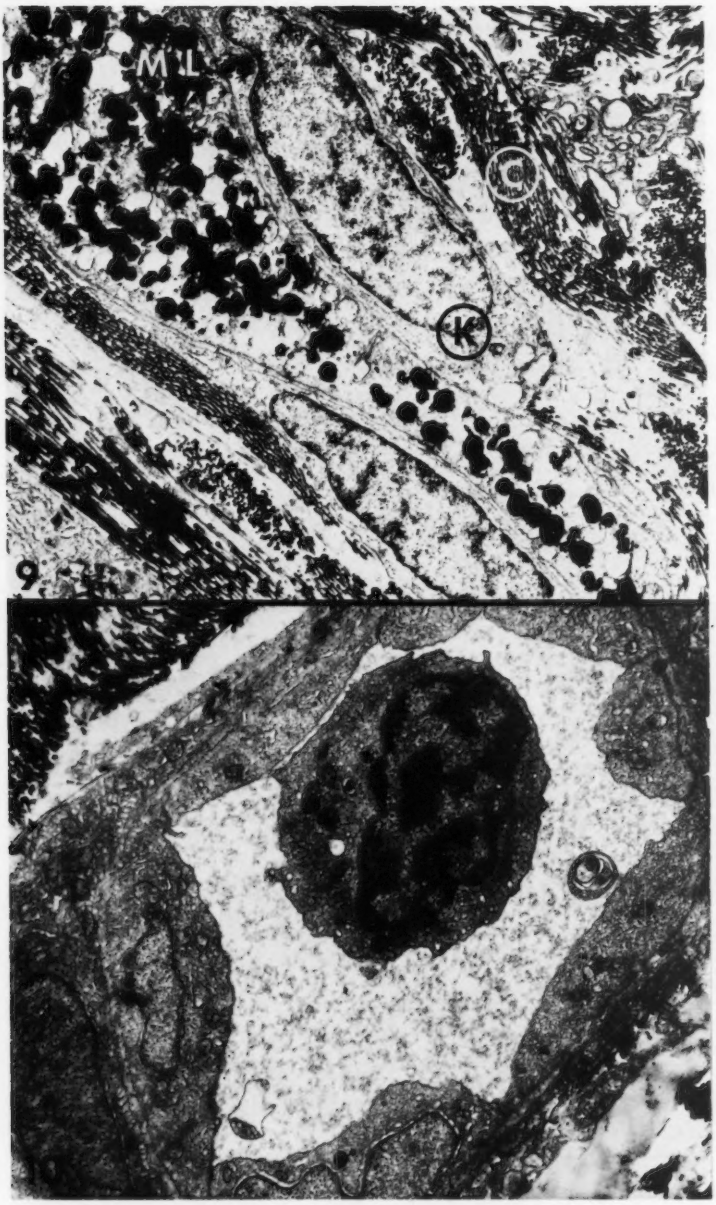


FIG. 9. Keratocytes (K), a melanocyte (ML) with pigment granules and collagen fibrils (C) of the limbal stroma. ×9000.

FIG. 10. Section through limbal stroma showing capillary with blood cell in lumen. ×10,500.

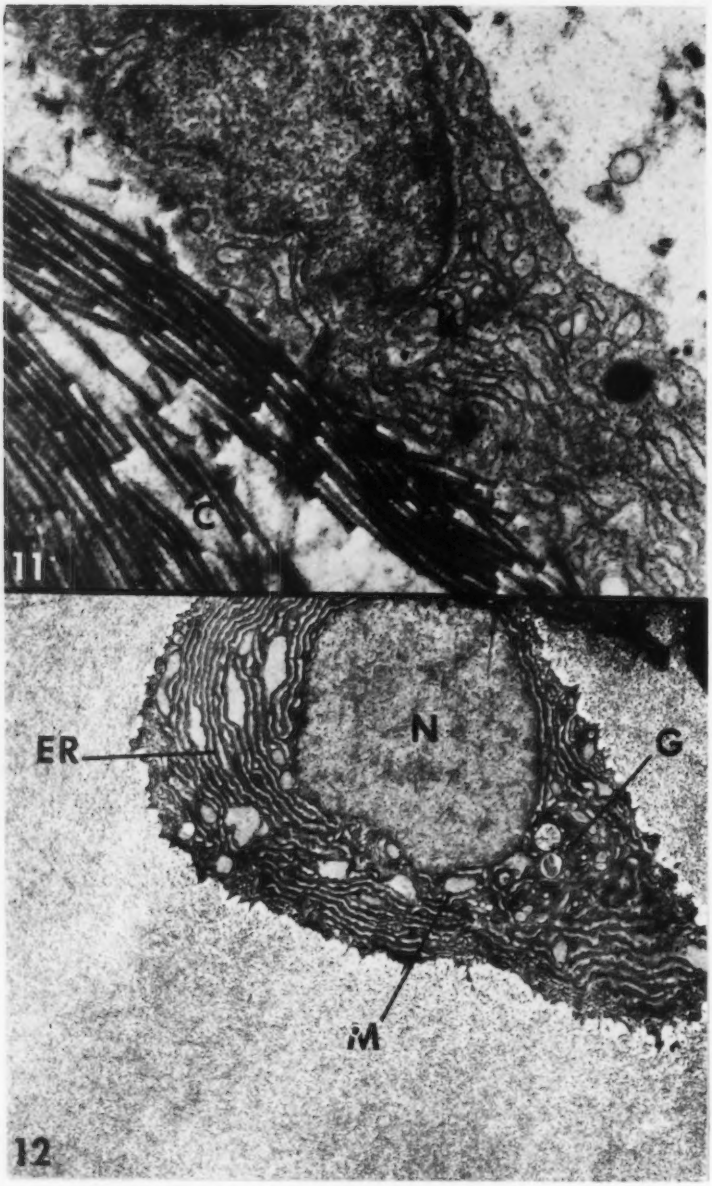


FIG. 11. A longitudinal section of a keratocyte (K) or stroma cell. Collagen fibrils (C) are seen in close proximity to the keratocyte. ×22,000.

FIG. 12. A cross-section of a keratocyte (central cornea) demonstrating a well-developed endoplasmic reticulum (ER), mitochondria (M), nucleus (N), and a prominent Golgi apparatus (G). ×6000.

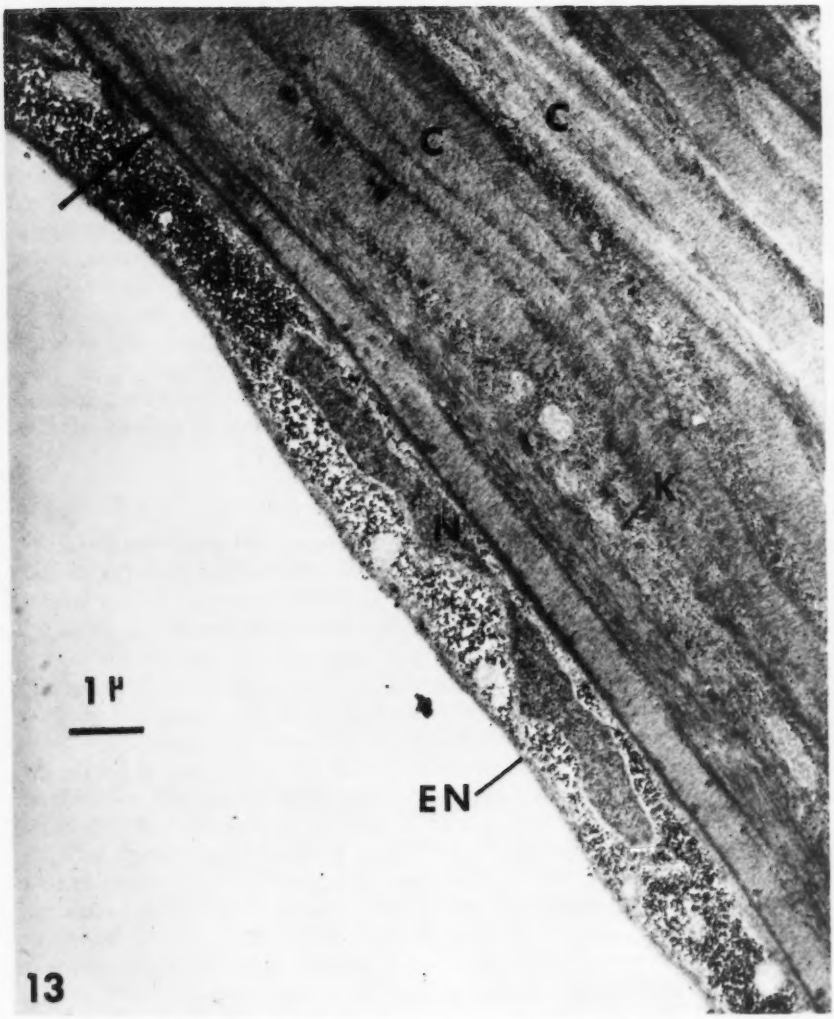


FIG. 13. Stroma and endothelium (EN) of central cornea. Laminar orientated collagen bundles (C) and keratocytes (K) comprise the stroma. The endothelial cells of the cornea contain glycogen (GL) particles and large, flattened nuclei (N) and possess a thin basement membrane (*arrow*). ×11,000.

Various types of collagen fibers and lamellae can be seen particularly well in the deeper layers of the peripheral corneal stroma (Fig. 9). In place of a single type of stroma cell as found in central corneal stroma (Fig. 11, 12, 13) the limbus contains a relatively high concentration of different cell types including melanocytes and keratocytes. In addition some capillaries were observed in the limbus (Fig. 10).

The keratocytes or stromal cells of the trout stroma are similar to the keratocytes found in other species of fish. Usually these cells are located between lamellae (Fig. 2, 11, 12, 13). A longitudinal section (Fig. 11) and a cross-section (Fig. 12) of a keratocyte show the many cytoplasmic organelles and endoplasmic reticulum.

The trout corneal endothelium (Fig. 13) consists of a flat layer of cells 1–2 μ thick and maintains a smooth flat inner surface in the cornea. The endothelial cells contain large, flat nuclei, few cytoplasmic organelles, and deposits of glycogen located throughout the cytoplasm. The basement membrane of the endothelium is not well defined or as electron-dense as the basement membrane of the basal epithelial cells.

DISCUSSION

A characteristic of the central trout cornea is that of uniformity. The three chief layers (epithelium, stroma, and endothelium) have smooth, parallel surfaces and the stroma collagen is oriented in layers which assume the plane of the cornea with the flat stroma cells lying within the contours of the lamellae.

In the limbus, by contrast, one observes irregularity. The epithelial cells lose their distinct areas of cytoplasm and possess microvilli. The collagen fibrils in the peripheral stroma appear more loosely packed and irregular in shape. Capillaries penetrate this region and melanocytes also appear in the stroma, for it is at this point the nutrients needed by the cornea are supplied for diffusion into the stroma. Loss of transparency of the cornea is also associated with this transitional area.

The corneal epithelium of trout contributes approximately 40% of the total thickness of the cornea in comparison with 40–55% in dogfish (Goldman and Benedek, 1967). In rabbit cornea, the epithelium is 30–40 μ thick and comprises 6–10% of the total corneal thickness (Prince, 1964, p. 90). This increased thickness is an adaptation of the fish to their environment and enables them to oppose the osmotic gradient (Smelser and Chen, 1954; Edelhauser et al., 1968). Microvilli in trout cornea appear to be located on the outer surface of the peripheral corneal epithelium, whereas in mammals microvilli have been observed across the entire outer corneal surface (Blümcke and Mogenroth, 1967). Bowman's membrane of the trout cornea, although randomly orientated to some extent, possesses greater organization than that observed in dogfish (Goldman and Benedek, 1967) and human cornea (Jakus, 1964). Trout cornea also appears to possess a greater number of keratocytes per stroma area than other species previously studied. Also, these keratocytes

appear to be active, as suggested by the large number of cytoplasmic inclusions and dilated sacs of endoplasmic reticulum. Their exact function, however, is unknown.

The corneal endothelium of trout appears very different from those of mammalian and avian species (Jakus, 1964). Specifically, there is a lack of cytoplasmic inclusions. Also, a Descemet's membrane as observed in other species is not readily descernible.

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REFERENCES

ALLISON, L. N. 1963. Cataract in hatchery Lake trout. Trans. Am. Fish. Soc., **92**: 34–38.

BLÜMCKE, S., AND K. MORGENROTH, JR. 1967. The stereo ultrastructure of the external and internal surface of the cornea. J. Ultrastructure Res., **18**: 502–518.

EDELHAUSER, H. F., J. R. HOFFERT, AND P. O. FROMM. 1966. Water permeability of normal and pathological lake trout corneas. Proc. Exptl. Biol. Med., **122**: 963–966.

1968. A comparative study of sodium permeability in Lake trout and rabbit corneas. Am. J. Physiol., **214**: 389–394.

EDELHAUSER, H. F., AND K. A. SIEGESMUND. 1968. The localization of sodium in the teleost cornea. Invest. Ophthalmol. (In press.)

GOLDMAN, J. N., AND G. B. BENEDEK. 1967. The relationship between morphology and transparency in the nonswelling corneal stroma of the shark. Invest. Ophthalmol., **6**: 574–600.

HOFFERT, J. R., AND P. O. FROMM. 1965. Biomicroscopic, gross, and microscopic observations of corneal lesions in the Lake trout, *Salvelinus namaycush*. J. Fish. Res. Bd. Canada, **22**: 761–766.

JAKUS, MARIE A. 1964. Ocular fine structure. Retina Foundation Institute of Biological and Medical Sciences. Monographs and Conferences Vol. I. 1st ed. Little, Brown, Boston.

PRINCE, J. H. 1964. The rabbit in eye research. Thomas, Springfield, Illinois.

SMELSER, G. K., AND D. K. CHEN. 1954. A comparative study of the structure and hydration properties of corneas adapted to air and aquatic environments. Acta XVII Concilium Ophthalmol., (Canada–USA), **1**: 490–499.

Roles of Olfaction and Vision in Choice of Spawning Site by Homing Adult Chinook Salmon (*Oncorhynchus tshawytscha*)[1]

By Alan B. Groves, Gerald B. Collins, and Parker S. Trefethen

U.S. Bureau of Commercial Fisheries
Biological Laboratory, Seattle, Wash.

ABSTRACT

An experiment was conducted to examine the roles of olfaction and vision in directing the choice of spawning site by homing adult chinook salmon (*Oncorhynchus tshawytscha*) on the lower Columbia River. Male fish that voluntarily entered the Spring Creek National Fish Hatchery were treated to occlude their olfactory or visual senses or both. Treated and untreated (control) fish were released upstream and downstream in the river, more than 19 km from the hatchery. Effects were assessed by analyzing returns to the hatchery and to other points.

Of 866 fish released, 348 or 40% were recovered; about half of them, or 176 returned to Spring Creek. Three per cent of the olfactory occluded, 23% of the visually occluded, and 46% of the control fish returned to Spring Creek. Of the fish recovered elsewhere, 77% were recovered at hatcheries and spawn-taking sites along the lower Columbia; 23% were recovered from sources unrelated to spawn taking.

Olfaction appeared to be the key sense that directed the return of these fish to Spring Creek; vision was held to be less important. Olfactory occlusion also reduced the recoveries at other spawn-taking sites, where blinded fish were recovered in appreciable numbers. Recovery of the control fish, especially the smaller ones, at other spawn-taking sites was associated with advancing sexual maturity.

INTRODUCTION

Adult salmon (*Oncorhynchus* spp.), after feeding and growing in widespread areas of the Pacific Ocean, typically migrate back to their native rivers and spawn in their natal waters. Dams or diversions created by the development of water resources can radically change the courses of rivers, confluences of tributaries, qualities of the flowing water, or other possible guideposts in these homing journeys. To foresee the effects of such changes on homing, a better understanding is needed of the mechanisms by which salmon are directed in their migrations — particularly of the sensory responses that guide the fish in those final stages when they choose specific spawning sites.

A favored premise is that final homing is based on olfaction, which enables salmon to detect distinctive odors in the waters originating from their destinations (Hasler and Wisby, 1951). An early experiment on the role of olfaction in homing of sockeye salmon (Craigie, 1926) was inconclusive. From more recent experiments, Wisby and Hasler (1954), using adult coho salmon (*O. kisutch*), concluded that olfactory occlusion interfered with ability to repeat a choice between two tributaries of a small stream and that olfaction enabled the fish to detect distinctive odors of the tributaries.

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We conducted our experiment on the lower Columbia River in the fall of 1960 to test the hypothesis that olfaction plays a decisive role in the choice of spawning sites by homing adult chinook salmon (*O. tshawytscha*) in a large river where the fish may face a number of alternatives. We also examined the role of sight in their choices. As did Wisby and Hasler, we occluded the sensory receptors of fish that had reached a spawning goal, displaced the fish, and then observed their sites of recovery.

EXPERIMENTAL PROCEDURES

Our work centered at the Spring Creek National Fish Hatchery, Underwood, Wash. (Fig. 1) on the main stem of the Columbia River, about 32 km above Bonneville Dam and about 256 km from the sea. Though the hatchery is situated on the river, its source of water for incubation and rearing is a series of adjacent springs. The same spring water fills the holding pond and flows out through a short fish ladder directly into the Columbia River — a physical arrangement suggesting that return of fish to this site may involve discrimination of a specific odor or other water property. The spring water flows from the entrance of the fish ladder at about 0.3 m^3/sec; during our experiment, the mean flow of the Columbia River was about 3000 m^3/sec (U.S. Army Corps of Engineers, MS, 1960).

All fish used in our study were adult males not needed in the normal spawning operation. These fish were captured, anesthetized with tricaine methanesulfonate (M.S. 222), marked with serially numbered disc tags, treated, and released on the same day they entered the hatchery fishway. One of four treatments was used on each fish: (1) olfactory occlusion; (2) visual occlusion; (3) olfactory and visual occlusion; and (4) control (no sensory occlusion, same handling procedures).

Our purpose in using visual occlusion (in addition to testing the role of sight in final homing) was to compare the fish with olfactory blocking with a group deprived of the use of a different major sensory organ in the event that shock from sensory loss alone altered behavior. The purpose of the combined treatment was to check the possibility that fish with olfactory occlusion might follow other migrants by sight and thereby obscure interpretation of the data.

To minimize effects of injury and to lessen the time required for treatment, we selected techniques which would block the reception of external stimuli rather than destroy sensory tissues. Olfactory occlusion was accomplished by packing petroleum jelly and cotton into the olfactory sac and suturing across the nares to retain the plugs. Visual occlusion was achieved by surgical removal of the optic lenses, which were replaced with an opaque mixture of petroleum jelly and carbon black to restrict the entrance of light. Treatment time was slightly over 1 min for olfactory occlusion and less for visual occlusion.

Although these methods did not eliminate the sensory organs, procedures that would have done so seemed unnecessarily severe. The destruction of

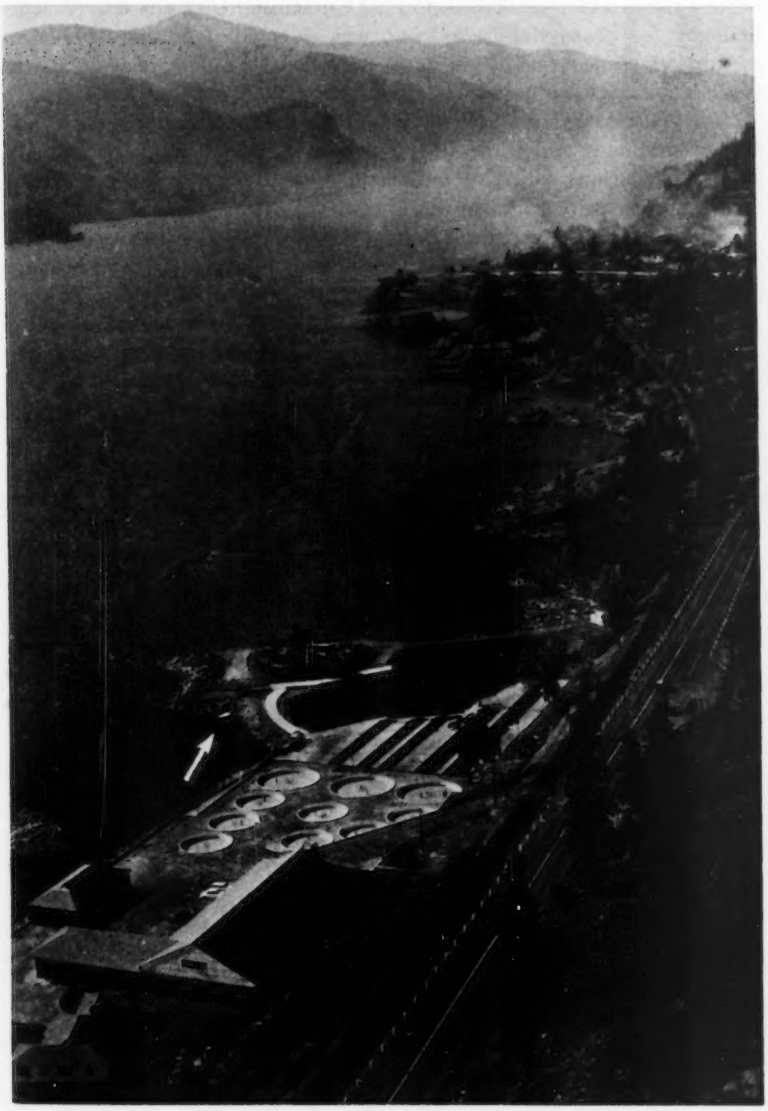

FIG. 1. Downstream view of the Columbia River with Spring Creek National Fish Hatchery in foreground. Holding pond for returning adult salmon is separated from river by earthen dikes; arrow points to water discharge of about 0.3 m^3/sec from entrance of small fishway which provides access to the pond.

either sense by severing of nerves would have required deep cuts; the removal of sensory tissue also appeared injurious. Chemical treatment was considered, particularly for destroying sight, but was rejected. Gunning (1959) found that intraocular injections of phemerol to destroy the sight of longear sunfish *Lepomis megalotis* (Rafinesque) caused gross behavioral changes and high mortality. Preliminary tests of our techniques indicated no adverse effects.

After treatment and while still anesthetized, equal numbers of fish subjected to the various forms of treatment were transported by tank trucks to release points away from Spring Creek. We released 866 treated and untreated fish at three sites during September 3–20, 1960. These sites (Fig. 2) were: (1) downstream on the north shore of the Columbia River at Stevenson, Wash.; (2) downstream on the south shore at Cascade Locks, Ore.; and (3) upstream on the north shore at Lyle, Wash. Our purpose in releasing fish at more than one place was to offset the possibility that released fish might return to Spring Creek by retracing their previous routes. All sites were more than 19 river km from the hatchery. Proportional numbers of fish from each treatment group and the control group were released daily at each site, so that the effects of advancing sexual maturity could not confound the results. Also, releases were staggered in time each day to offset the possible effects from unknown factors that might vary within the day.

EFFECTS OF OLFACTORY AND VISUAL OCCLUSION

Tags were recovered at the Spring Creek hatchery, and at other hatcheries or spawn-taking sites, from such activities as sport fishing upstream and downstream from Spring Creek, and from the commercial fishery below Bonneville Dam. A few tags were returned from widely scattered points in the Columbia River and its tributaries.

Tags were recovered from 348 fish (Table I), or 40% of the 866 released. About half (176) of the tag recoveries were fish that returned to Spring Creek National Fish Hatchery.

Returns to Spring Creek

Most of the tags from the Spring Creek hatchery were collected during spawn taking and the dates of return to the hatchery were not known. Tags from the fish that returned from September 4 through 20 were recovered when the fish first re-entered the hatchery fishway from the Columbia River. We examined these fish individually for retention of olfactory plugs and general physical condition. After September 20 (when the releases were ended), hatchery operations precluded recovery and examination of individual fish.

About 50% of the control fish returned to Spring Creek from each of the downstream sites and 37% from the upstream site (Table I). About half as many blinded fish as control fish returned from each release point.

Six fish with olfactory occlusion returned — five from the downstream release site on the north shore and one from the downstream release site on

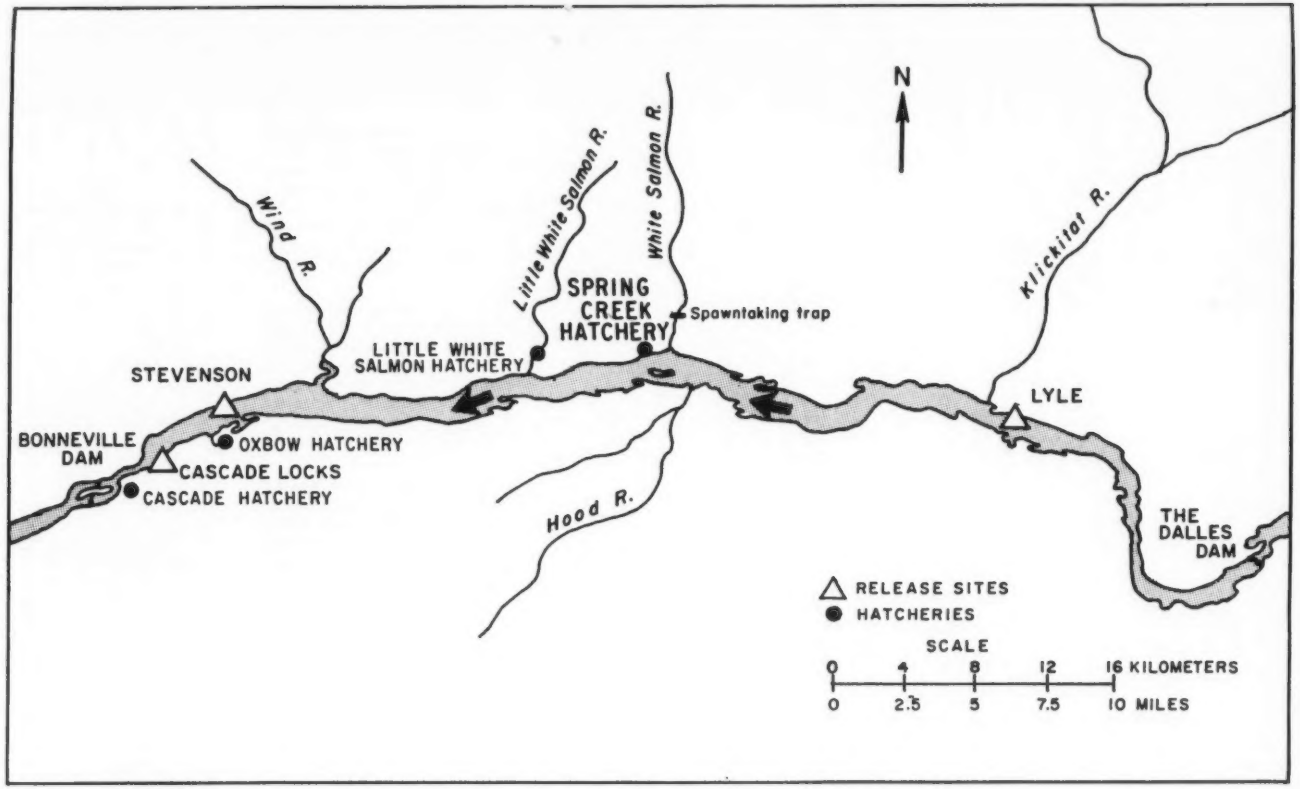

FIG. 2. Locale of homing experiment on Columbia River.

TABLE I. Numbers of fall-run chinook salmon recovered, September 4–October 11, at various sites on lower Columbia River after displacement to three sites from Spring Creek hatchery and blocking of sensory receptors.

Release site	Recovery site	No. of recoveries, by treatment: Olfactory occlusion	Visual occlusion	Olfactory and visual occlusion	Control fish	Totals
		(75)	(96)	(74)	(96)	(341)
Downstream from Spring Creek on north shore of Columbia River at Stevenson, Wash.	Spring Creek Hatchery	5	22	1	48	76
	Oxbow Hatchery	1	11	–	9	21
	Cascade Hatchery	6	2	–	2	10
	Little White Salmon Hatchery	–	1	–	5	6
	White Salmon River	–	7	–	1	8
	Other spawn-taking sites[a]	1	2	–	–	3
	Other than spawn taking[b]	8	–	7	1	16
	Totals recovered	21	45	8	66	140
		(77)	(96)	(76)	(96)	(345)
Downstream from Spring Creek on south shore of Columbia River at Cascade Locks, Ore.	Spring Creek Hatchery	1	24	1	46	72
	Oxbow Hatchery	3	14	–	23	40
	Cascade Hatchery	15	4	1	4	24
	Little White Salmon Hatchery	–	2	–	–	2
	White Salmon River	–	4	–	1	5
	Other spawn-taking sites[a]	1	4	–	–	5
	Other than spawn taking[b]	8	–	8	–	16
	Totals recovered	28	52	10	74	164
		(41)	(49)	(41)	(49)	(180)
Upstream from Spring Creek on north shore of Columbia River at Lyle, Wash.	Spring Creek Hatchery	–	10	–	18	28
	Oxbow Hatchery	–	–	–	–	–
	Cascade Hatchery	1	–	–	–	1
	Little White Salmon Hatchery	–	–	–	–	–
	White Salmon River	–	3	–	1	4
	Other spawn-taking sites[a]	–	1	–	2	3
	Other than spawn taking[b]	2	2	3	1	8
	Totals recovered	3	16	3	22	44
Grand total:	Released	(193)	(241)	(191)	(241)	(866)
	Recovered	52	113	21	162	348

[a]Kalama River Hatchery, Bonneville Hatchery, and spawn-taking facilities on the Klickitat River.
[b]Most recoveries were from sport fishermen and from the commercial fishery below Bonneville Dam.

the south shore. Two fish with visual and olfactory occlusion returned — one from each downstream release point. These eight fish were recovered after September 20 and hence were not examined for retention of olfactory plugs.

Only controls and blinded fish returned from the upstream release site. Of the 482 fish released from all sites without olfactory occlusion, 168, or 35%, returned to Spring Creek; of the 384 released with olfactory occlusion (191 also blinded), however, only 8 (2%) returned.

Fish that returned to Spring Creek from September 4 through 20 were from the control and blinded groups only, but this provided some data on elapsed time between release and return to Spring Creek (Table II). The mean time was about 5 days for control fish and 7 days for blinded fish. No blinded fish returned in less than 4 days, but 10 control fish reappeared within 3 days.

TABLE II. Numbers of control (C) and blinded (B) fish that returned from three release sites to Spring Creek hatchery from September 4 to 20, according to number of days after release.

Days out	No. of fish returning from release sites							
	Stevenson, Wash.		Cascade Locks		Lyle, Wash.		Total	
	C	B	C	B	C	B	C	B
1	–	–	1	–	–	–	1	–
2	–	–	1	–	2	–	3	–
3	4	–	2	–	–	–	6	–
4	6	2	4	–	–	–	10	2
5	2	1	5	1	1	–	8	2
6	1	2	6	1	3	2	10	5
7	2	1	3	2	–	1	5	4
8	2	2	1	3	–	–	3	5
9	–	1	–	1	–	–	–	2
10	–	–	1	–	–	1	1	1
11	1	–	–	1	–	–	1	1
12	–	–	–	–	1	–	1	–
Total fish	18	9	24	9	7	4	49	22
Mean days out							5.5	7.0

The return to Spring Creek of numerous control and blinded fish from all release points, but of few fish with olfactory occlusion, indicated that the return was accomplished more by an olfactory response than by a visually guided retracing of previously traveled routes. The return of only control and blinded fish from the upriver releases additionally suggested the role of olfaction as an orienting mechanism. If fish released upstream had moved back down the river far enough to pass Spring Creek, perhaps only those without olfactory occlusion (control and blinded fish) were able to perceive odors from the

hatchery and thereby to respond by re-entering the fishway. Taft and Shapovalov (1938) reported downstream movements of fish that had bypassed their homestream spawning site. Possibly the change in behavior they observed was the result of loss to the fish of orienting odor cues from their home waters.

Fish with olfactory occlusion that returned from downstream may have done so because of ineffective treatment, but on the other hand, their return may have reflected the locations of their release points. Of the eight fish with olfactory occlusion that returned to the hatchery, six were from the north-shore release site on the same side of the river as Spring Creek; these fish may have followed along the shoreline as they traveled upstream. A tendency of migrating adult salmon to orient near the shoreline in the lower Columbia River was reported by Johnson (1960).

Similar ratios between control and blinded fish that returned to Spring Creek from the three release sites (Stevenson, 48:22; Cascade Locks, 46:24; and Lyle, 18:10) suggested that, in contrast to the dominant role of olfaction, vision had a secondary role in the return. The blinded fish were handicapped during their return trip; this fact was indicated by fewer recoveries, delay, and a usually battered appearance on arrival at Spring Creek. They nevertheless reappeared from each release site in appreciable numbers, whereas few unblinded fish with blocked olfactory organs returned.

Recoveries at Other Locations

Of 172 tags recovered from points other than Spring Creek, 132 (or 77%) were from hatcheries and other spawn-taking facilities; the remaining 40 (or 23%) were from other sources (Table I). These returns were affected by sensory treatment. From releases of control and visually occluded fish, about 96% of the recoveries from sites other than Spring Creek (103 fish out of 107) were from spawn taking. Of the fish released with olfactory occlusion, 61% of the recoveries (28 out of 46) were from spawn-taking activities. Fish that had both senses occluded yielded rates of recovery lower than other groups, and 95% of the recoveries (18 out of 19) were from activities other than spawn taking.

Tagged fish recovered from all spawn-taking sites were usually trapped upon entry. Thus since fish could not leave, recoveries from sites other than Spring Creek were not necessarily a measure of straying but may reflect as well the amount of fish cultural activity in the area of the experiment.

Of the 132 recoveries from spawn-taking sites other than Spring Creek, 121 were within 24 km upstream from Bonneville Dam. Of the 121, 96 were from two hatcheries — Oxbow Hatchery, about 3 km upstream from the release site at Cascade Locks; and Cascade Hatchery, about the same distance downstream from that site. Of the tags recovered from Oxbow Hatchery, 93% were from control and blinded groups. Only 35% of the recoveries at Cascade Hatchery were control and blinded fish; 65% were fish with olfactory occlusions. These two hatcheries accounted for nearly all of the 28 fish with olfactory occlusion recovered from spawn-taking sites other than Spring Creek;

4 were recovered at Oxbow, and 22 at Cascade Hatchery. The remaining 2 were from Kalama Hatchery, about 144 km downstream from Bonneville Dam.

The orienting role of olfaction also was indicated when the fish chose spawn-taking sites other than Spring Creek. When the olfactory organs were blocked, fish were less likely to appear at such places. The only exception was at Cascade Hatchery where a number of fish with olfactory occlusions were recovered. The reason is unknown.

EFFECTS OF TIME OF RELEASE AND SIZE OF FISH ON RECOVERY

Recovery of the untreated control fish was affected by the time of release in the 18-day experiment and by the size of the fish (Fig. 3). From early releases of the controls, most recoveries were from Spring Creek, but the percentages

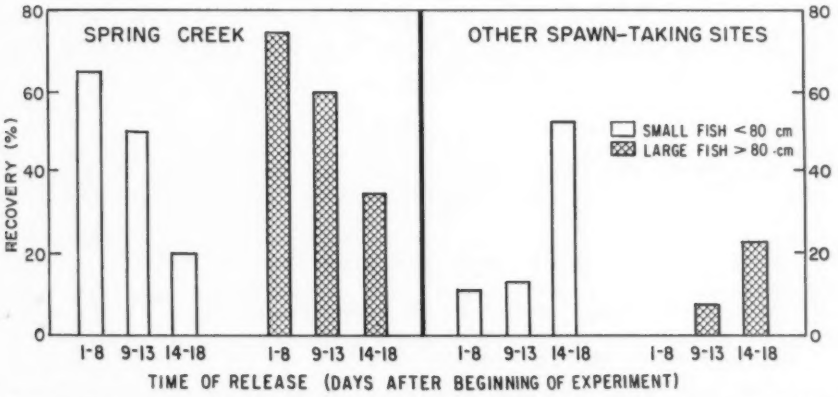

FIG. 3. Recoveries of control fish in two size-ranges at Spring Creek and other spawn-taking sites according to time of release.

recovered from later releases declined at Spring Creek and increased elsewhere. This change of behavior accompanied increased sexual maturity of fish released later and suggested that specific homing by olfaction may be masked during final stages of maturation — perhaps by the spawning drive itself — and that olfaction then may enable the fish to detect and seek other places where maturing fish are present.

Size of the control fish ranged from 55 to 106 cm (fork length). Most control fish that were recovered from spawn-taking sites other than Spring Creek were shorter than 80 cm. Although small fish were recovered at Spring Creek and elsewhere from all releases, most recoveries of the small fish released in the last 5 days were from sites other than Spring Creek. On the other hand, of control fish larger than 80 cm released throughout the experiment, the percentage of recovery was consistently higher at Spring Creek than at other sites; most recoveries of larger fish released in the last 5 days were still made at Spring Creek.

CONCLUSIONS

Olfaction appeared to be the major sensory mechanism directing the final migratory movements of chinook salmon in the Columbia River.

Olfactory occlusion reduced the return of the displaced fish to Spring Creek by a factor of over 10; this reduction indicated the primary role of olfaction in directing return of salmon to the hatchery. Olfactory occlusion also reduced the numbers of fish that arrived at most spawn-taking sites other than Spring Creek; olfaction probably also played a primary role in guiding fish to alternate sites.

Blinding reduced the return of the fish by a factor of 2; vision seemed to have a contributory but less essential role in the return. Blinding alone did not reduce the recovery of fish at spawn-taking sites other than Spring Creek.

Occlusion of both olfaction and vision reduced the recovery from all sources.

Recovery of control fish from sites other than Spring Creek increased with advancing sexual maturity and was more evident in small fish (less than 80 cm, fork length) than in large fish.

REFERENCES

CRAIGIE, E. HORNE. 1926. A preliminary experiment upon the relation of the olfactory sense to the migration of the sockeye salmon (*Oncorhynchus nerka*, Walbaum). Trans. Roy. Soc. Canada, 3rd Ser., **20**(Sec. 5): 215–224.

GUNNING, GERALD E. 1959. The sensory basis for homing in the longear sunfish, *Lepomis megalotis megalotis* (Rafinesque). Invest. Indiana Lakes Streams, **5**(3): 103–130.

HASLER, ARTHUR D., AND WARREN J. WISBY. 1951. Discrimination of stream odors and its relation to parent stream behavior. Am. Naturalist, **85**(823): 223–238.

JOHNSON, JAMES H. 1960. Sonic tracking of adult salmon at Bonneville Dam, 1957. U.S. Fish Wildlife Serv., Fish Bull., **60**: 471–485.

TAFT, A. C., AND LEO SHAPOVALOV. 1938. Homing instinct and straying among steelhead trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*). Calif. Fish Game, **24**(2): 118–125.

U.S. ARMY CORPS OF ENGINEERS. MS, 1960. Annual fish passage report, North Pacific Division, Bonneville, The Dalles and McNary Dams, Columbia River, Oregon and Washington, 1960. U.S. Army Engineer Districts, Portland and Walla Walla, Corps of Engineers. xiii + 53 p.

WISBY, WARREN J., AND ARTHUR D. HASLER. 1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). J. Fish. Res. Bd. Canada, **11**(4): 472–478.

A Review of the Morid Fish Genus *Halargyreus* with First Records from the Western North Atlantic[1]

By Wilfred Templeman

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

Three specimens of *Halargyreus johnsonii* taken on the southwestern and southeastern slopes of the Grand Bank in 1959 and 1964 are apparently the first records of this species and genus from the western Atlantic. These specimens are compared with the holotypes of *H. johnsonii* Günther and of *H. brevipes* Vaillant and with the syntypes of *H. affinis* Collett and also with specimens identified as *H. affinis* from the north-central and northeast Atlantic and with specimens of *H. johnsonii* from Madeira and New Zealand. These three nominal species are also compared. Is it concluded that for the present all North Atlantic specimens may be referred to *H. johnsonii* and that the other two species names should be considered as junior synonyms of *H. johnsonii*.

The New Zealand specimens of *Halargyreus*, described by Günther (1887, Challenger Rept., 22(Zoology), p. 1–268) as *H. johnsonii*, have higher numbers for some meristic characters than Atlantic specimens of *H. johnsonii* but these differences are not too great to be possibly due to environmental differences. Pending the study of additional specimens in better condition, these New Zealand specimens are tentatively allowed to remain as *H. johnsonii*.

INTRODUCTION

Three specimens of *Halargyreus johnsonii* Günther, 1862, family Moridae, were taken by the *A. T. Cameron* on the southern part of the Grand Bank, one on May 5, 1959, and two on November 24, 1964 (Table I). These are apparently the first records of this species and genus from the western Atlantic.

Günther (1862) established the genus *Halargyreus* and described the species *Halargyreus johnsonii* from a specimen lacking the posterior part of the tail, obtained at Madeira from the stomach of a *Saccopharynx*. He later (Günther, 1887) obtained a few specimens from New Zealand, also in a very poor state of preservation, and from these supplied some new meristic information but no further body proportions. The original description could not provide either a total or a standard length. No figure of this species was supplied. Maul (1952) reported on a specimen of *H. johnsonii* from Madeira and four other specimens have been obtained from Madeira (Table I).

Vaillant (1888) described *Halargyreus brevipes* on a single specimen from the eastern Atlantic off Morocco. In this specimen all fins were in poor condition.

The third species, *Halargyreus affinis*, was described by Collett (1904, 1905) on the basis of five specimens from a collection of 106 taken on the

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TABLE I. Records of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis* from the North Atlantic.

	Reference	Date of capture	Locality of capture	Position N lat	Position W long	Depth of capture (*m*)	Bottom temp (*C*)	Total length fish (*mm*)	No. of specimens	Remarks
				Halargyreus johnsonii Günther, 1862						
1.	Günther (1862)	Before June 4, 1861[a]	Madeira	–	–	–	–	–	1	Found in stomach of *Saccopharynx*. Posterior part of tail missing
2.	Maul (1952)	Before 1952	Madeira. Câmara de Lobos	–	–	At least ca.500	–	313[b]	1	From fish market. Caught on lines set for *Aphanopus carbo*
3.	Letter from Dr D. M. Cohen July 1967[c]	–	Madeira	–	–	–	–	390	1	From Funchal. (Now in the museum at Monaco)
4.	G. E. Maul (letter, Aug. 1, 1967)[c]	May 24, 1955	Madeira	–	–	At least ca.500	–	432[b]	1	From fish market, Funchal. Caught on lines set for *Aphanopus carbo*
5.	" "	June 17, 1955	Madeira	–	–	"	–	357[b]	1	" "
6.	" "	Aug. 14, 1965	Madeira	–	–	"	–	409[b]	1	" "
				Halargyreus brevipes Vaillant, 1888						
7.	Vaillant (1888)	1883	Off Mazaghan (El Jadida), Morocco, 1319 m	–	–	350	8	350+[d]	1	*Talisman*, in small trawl
				Halargyreus affinis Collett, 1904						
8.	Hjort (1909)	Aug. 12, 1902	S slope Faroe Bank	59°28′	8°01′	1061–1256	8.07[e]	At least 217–267[b,f]	7[g]	*Michael Sars*, trawl
9.	"	Aug. 12, 1902	S slope Faroe Bank	59°23′	7°50′	1074	8.07[e]	–	5	" "
10.	"	Aug. 14, 1902	Faroe Slope	61°07′	9°33′	777–841	–	At least 112–250[b,f]	94[g]	" "
11.	Holt & Byrne (1908)	Feb. 5, 1907	Irish Atlantic Slope	51°18′	11°50′	960–1100	8.35	278	1	*Helga*, beam trawl. Salinity 35.50‰

12.	Blacker (1962)	July 9, 1960	Irish Atlantic Slope	52°00′	13°34′	490–550	–	70–120	34	*Ernest Holt*, trawl
13.	Blacker (1962)	May 31, 1961	Rockall Bank	56°08′	16°50′	461	–	90	1	*Ernest Holt*, trawl
14.	Krefft (1965)	Mar. 18, 1963	S Icelandic Slope	63°45′	26°40′	760–810	5.80	170–280[h]	6	*Anton Dohrn*, otter trawl (bottom), Station No. 477/63
15.	Krefft (1966)	Jan. 22, 1964	Rosemary Bank	59°21′	10°22′	720–730	8.7	80–140[h]	4	Station No. 12/64
16.	"	Jan. 24, 1964	Lousy Bank	60°21′	11°54′	710–740	8.6	130–150[h]	5	" 16/64
17.	"	Jan. 26, 1964	Bill Bailey Bank	60°49′	9°56′	730	8.3	100–130[h]	28	" 21/64
18.	"[e]	Mar. 3, 1964	Porcupine Bank	52°22′	12°52′	600	10.23	90[h,i]	3	" 220/64
19.	"	Mar. 17, 1964	S Icelandic Slope	63°13′	25°50′	810	6.5	200–260[h]	8	" 223/64
20.	"	Mar. 18, 1964	W Icelandic Slope	65°19′	27°49′	800–840	5.92	140–340[h]	54	" 225/64
21.	"	Apr. 9, 1964	S Icelandic Slope Selvogs Bank – S	63°06′	21°33′	750–800	ca.7.0	140–270[h]	103[j]	" 285/64
22.	Krefft (1967)	Apr. 20, 1965	W Icelandic Slope	64°07′	27°16′	800	5.89	190–240[h]	4	" 410/65
23.	Krefft (1967)	Apr. 24, 1965	S Icelandic Slope	62°43′	24°30′	730–780	5.43	110–310[h]	158	" 413/65
24.	Dr G. Krefft, Nov. 18, 1966 (letter)[e]	Apr. 27, 1965	"	63°28′	26°16′	750–780	5.77	200[h]	1	" 417/65
25.	Krefft (1967)	Apr. 28, 1965	"	63°05′	23°38′	700	5.90	100–120[h]	2	" 421/65
26.	"	Apr. 29, 1965	"	63°00′	22°06′	800	–	130–290[h]	372	" 426/65
27.	"	Apr. 30, 1965	"	63°03′	20°30′	700–750	5.19	130–270[h]	206	" 430/65
			***Halargyreus johnsonii* from the Northwest Atlantic**							
28.	Author[c]	May 5, 1959	SW Slope Grand Bank	43°11′	51°39′	705–785	4.11	305	1	*A. T. Cameron*, otter trawl (bottom) (V. M. Hodder, scientist-in-charge)
29.	Author[c]	Nov. 24, 1964	SE Slope Grand Bank	43°33′	48°49′	585–670	3.81	225, 263	2	*A. T. Cameron*, otter trawl (bottom) (E. J. Sandeman, scientist-in-charge)

[a]Date of accession, British Museum.
[b]Standard length.
[c]Previously unpublished records.
[d]Caudal fin rays broken off.
[e]Bottom temperature from Koefoed (1927).
[f]Three specimens from each set in University of Copenhagen museum, five of them carrying the label *H. johnsonii* and one *H. affinis*. Information from Dr D. M. Cohen by letter Aug. 9, 1967.
[g]The five specimens of *H. affinis* reported by Collett (1904, 1905) evidently came from these sets.
[h]Measurements to the centimetre below.
[i]Information from Dr G. Krefft Nov. 18, 1966. Omitted from the published record of Krefft (1966).
[j]103 correct, from Dr G. Krefft Apr. 11, 1967. The figure 173 in Krefft (1966) is incorrect.

Faroe slopes by the *Michael Sars* (Table I; Hjort, 1909; also Koefoed, 1927). Since that time an additional 990 specimens of *H. affinis* have been reported from the northeast and north-central Atlantic (Table I).

The three specimens of *H. johnsonii* from the Grand Bank examined by the author are within or overlapping the range of Collett's *H. affinis* for all meristic characters examined by both authors (Table II). They are also within, overlapping, or close to the range for all of the small number of body proportions of *H. affinis* as measured by Collett (Table III) and agree with Collett's excellent figure of *H. affinis* (Collett, 1905). More comparisons can be made with Collett's *H. affinis* than with Günther's holotype of *H. johnsonii*, and all North Atlantic *Halargyreus* except the holotypes of *H. johnsonii* and *H. brevipes* and one specimen of *H. johnsonii* described by Maul (1952) have been reported as *H. affinis*. Hence, in the preliminary comparisons with *H. johnsonii* and *H. brevipes*, these Grand Bank specimens of *H. johnsonii* are treated as *H. affinis* for purposes of discussion and provide some meristic characters and many body proportions missing from Collett's description of this nominal species.

METHODS OF MEASUREMENT AND COMPARISON

In the following descriptions, unless it is otherwise stated, the methods of measurement, etc. followed by the author are those of Hubbs and Lagler (1958). Apart from total lengths, standard lengths, caudal fin lengths, and the extension of the lower jaw beyond the upper, which are shortest distances between perpendicular parallel planes, other measurements are direct distances between points.

Collett (1905) in his measurements of *H. affinis* may have used the anterior point of the lower jaw instead of the snout measurement. In his diagnosis he says: "Under jaw longest. Eye included in head length about 3.8 times." Later he gives actual head and eye lengths for five specimens and these eye lengths are included on the average 3.84 times in the head lengths. Still later, in the detailed description he says: "Eye included in the head's greatest length (measured to the point of the lower jaw) about 3.8 times."

In Table III head lengths have been used as a basis and hence true body proportion percentages may be slightly larger for Collett's *H. affinis* than those shown in this table. However, the change would be small. On the measurements of both head lengths in the Grand Bank specimens (Table III), head length from the snout is 1.9% less than that from the tip of the chin tubercle. Hence for Collett's fish the true percentages based on head lengths, if his head lengths were from the tip of the lower jaw, would be about 2% (of the present values) greater than those shown in Table III if the head lengths used as a base for the percentages were from the snout. These changes would make no difference in our conclusions.

For the holotype of *H. johnsonii* no standard length was available because the posterior part of the tail was missing. Also standard length was not included in Vaillant's original measurements of *H. brevipes*. Collett provided

TABLE II. Meristic and other number characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*.

TABLE II. Meristic and other number characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*.

Item no.	Locality of capture	Date of capture	Reference	Total length, *mm*	Standard length, *mm*	No. of 1st dorsal rays	No. of 2nd dorsal rays[a]	No. of 1st anal rays[b]	No. of 2nd anal rays[a,b]	No. of both anals, rays	No. of pectoral rays	No. of pelvic rays	No. of vertebrae[c]	No. of caudal vertebrae[d]	No. of gill rakers on 1st arche	No. of branchiostegals	No. of pyloric caeca	Source of specimens examined by the author
								H. johnsonii Günther, 1862 (holotype)										
1.	Madeira	1862 or earlier	Günther (1862)	f	f	7	f	17	f	f	–	5	f	f	–	7	–	
1.	"	"	Author	f	f	7	f	19	f	f	18	5	f	f	6+17	7	–	British Museum (N.H.)
								H. johnsonii from Madeira										
2.	"	Before 1952	Maul (1952)	–	313	1g+7	49	–	–	42	18	5	–	–	?+17	7	10	
2.	"	"	Author	f	317	1g+7	49	21	21	42	18	5	53	32	6+18	7	9	Museu Funchal
3.	"	May 1955	"	f	432	1g+7	51	20	22	42	17	5	52	32	6+16	7	9	" "
4.	"	June 1955	"	f	357	1g+7	52	22	21	43	18	5	53	32	6+18	7	8	" "
4 A.	"	Aug. 14, 1965	"	f	406	1g+7	50	21	21	42	18	5	53	32	7+18	7	f	" "
								H. johnsonii from New Zealand										
5.	Cook Strait, New Zealand	1873 or earlier	Günther (1887)	–	–	7	57	–	–	41	–	–	–	–	–	–	–	
6.	Cook Strait, New Zealand	1873 or earlier	"	–	–	7	47	–	–	41	–	–	–	–	–	–	–	
7.	New Zealand	Probably 1873 or earlier	"	–	–	7	55	–	–	46	–	–	–	–	–	–	–	
5.	Cook Strait, New Zealand	1873 or earlier	Author	210+f	194	1g+6	58	22	ca.29	ca.51	19	5[h]	57	34	5+15	7	f	British Museum (N.H.)
6.	Cook Strait, New Zealand	1873 or earlier	"	218	196	1g+7	56	23	24	47	19	5	56	35	6+15	7	f	" "
7.	New Zealand Inst., Wellington	Probably 1873 or earlier	"	264	243	1g+7	56	22	27	49	18	5	56	34	5+15	7	f	" "

(*Continued*)

TABLE II. Meristic and other number characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*. — (*Concluded*)

Item no.	Locality of capture	Date of capture	Reference	Total length, *mm*	Standard length, *mm*	No. of 1st dorsal rays	No. of 2nd dorsal rays[a]	No. of 1st anal rays[b]	No. of 2nd anal rays[a,b]	No. of both anals, rays	No. of pectoral rays	No. of pelvic rays	No. of vertebrae[c]	No. of caudal vertebrae[d]	No. of gill rakers on 1st arch[e]	No. of branchiostegals	No. of pyloric caeca	Source of specimens examined by the author
									H. brevipes Vaillant, 1888 (holotype)									
8.	Off Mazaghan (El Jadida), Morocco	1883	Vaillant (1888)	350	–	8	56	26	22	48	–	5	–	–	–	7	–	
8.	Off Mazaghan (El Jadida), Morocco	1883	Author	352+[f]	333	1ʁ+7	52	20[i]	23[i]	43[i]	18	5	51	30	7+17	7	10	Muséum National d'Histoire Naturelle, Paris
									H. affinis Collett, 1904 (syntypes)									
9.	Faroe Slope	Aug. 1902	Collett (1905)	251	–	7	51	–	–	42	–	–	–	–	–	–	–	
10.	"	"	"	261	–	6	53	–	–	44	–	–	–	–	–	–	–	
11.	"	"	"	261	–	1ʁ+7	50	–	–	42	–	–	–	–	–	–	–	
12.	"	"	"	262	–	1ʁ+7	50	–	–	41	–	–	–	–	–	–	–	
13.	"	"	"	270	–	1ʁ+7	51	–	–	42	–	–	–	–	–	–	–	
General	"	"	"	–	–	–	–	ca.20–22	–	–	17–18	5	–	–	?+17	7	9(11[j])	
									H. affinis									
14.	Irish Atlantic Slope	July 1960	"	[f]	110	1ʁ+7	52	21	22	43	19	5	53	–	7+17	–	–	British Museum (N.H.)
15.	Irish Atlantic Slope	July 1960	"	[f]	94	1ʁ+7	53	21	23	44	18	5	53[k]	–	6+18	–	–	(Collection by R. W. Blacker,
16.	Rockall Bank	May 1961	"	[f]	81	1ʁ+7	54	21	23	44	–	5	54	–	6+18	–	–	Lowestoft Laboratory)
17.	Icelandic Slope	Mar. 1964	"	[f]	211	7	53	20	26	46	19	5	54	33	6+18	7	9	Institut für

17.	Icelandic Slope, *Anton Dohrn* Station 225, 65°19′N, 27°49′W, 800–840 m	Mar. 1964	"	f	211	7	53	20	26	46	19	5	54	33	6+19	7	9	Institut für Seefischerei, Hamburg (Dr G. Krefft)
18.	"	"	"	f	218	7	54	22	25	47	18	5	54	32	7+21	7	10	" "
19.	"	"	"	f	249	1g+6	ca.53	20	26	46	17	5	53	32	6+16	7	9	" "
20.	"	"	"	f	267	1g+8	49	21	22	43	18	5	52	31	6+15	7	10	" "
21.	"	"	"	f	274	1g+7	50	19	23	42	19	5	53	32	6+17	7	10	" "
22.	"	"	"	f	297	1g+7	52	22	22	44	19	5	53	32	6+18	7	10	" "
				H. johnsonii from the Northwest Atlantic														
23.	SW slope Grand Bank	May 1959	Author		305	274	1g+7	53	19	22	41	18	5	54	33	6+18	7	10	Biological Station St. John's, Nfld.
24.	SE slope Grand Bank	Nov. 1964	"		225	200	1g+6	52	20	23	43	18	5	53	31	6+16	7	9	" "
25.	"	Nov. 1964	"		263	236	1g+7	52	21	23	44	18	5	54	33	6+17	7	8	" "

[a]In author's counts, last 2 rays separate and counted separately.

[b]In author's counts, first anal counted to and including the smallest ray between the anals, and 2nd anal from the next ray which is larger (Fig. 9). Because there is no break or absolute distinction between 1st and 2nd anals, the anal fin may be considered as one and most attention should be paid to the total anal count. The 1st anal counts, although approximate, are useful for comparison with the holotype of *H. johnsonii* for which only the count of the 1st anal is available.

[c]In author's counts, including urostylar half-vertebra + hypural as 1 vertebra.

[d]Determined from radiographs and at least in some cases could be 1 less.

[e]Including rudimentary rakers.

[f]Unsuitable for this character.

[g]Rudimentary spine at anterior base 1st dorsal (Fig. 7). Collett (1905) says that in some cases there is a rudimentary spine in front of the first long dorsal ray. For Table II, I have not investigated or decided the question of whether this is in fact a spine or a ray and the 1 in 1+7 etc. for the 1st dorsal is used merely to denote the presence of the rudimentary spine or ray in front of the longer rays.

[h]Five on left but 6 on right.

[i]Second to 5th 2nd anal rays missing but could be counted. There is also a pterygiophore without a corresponding ray in front of the 1st anal ray. This was not counted. Other ray counts satisfactory with possible exception of pectoral.

[j]In one specimen.

[k]Each of two additional specimens of *H. affinis* (one of 95 and one of 105 mm S.L.) from Blacker's collection on the Irish Atlantic Slope July 1960, and not recorded in Table II, also possessed a vertebral count of 53. In another group of radiographs of seven of Blacker's specimens from this cruise, loaned to me by Dr D. M. Cohen, the vertebral counts were: 52(1), 53(4), and 54(2).

NOTE RE SCALE COUNTS: Vaillant (1888) for *H. brevipes* records scales in the lateral line as ca. 122 and scales above and below the lateral line, 7 and 30. Collett (1905) for *H. affinis* notes scales above and below the lateral line, 8–10 and 30.

GENERAL NOTE. I have used radiographs for vertebral counts with direct checking on the specimen for the three St. John's Station specimens. For fin rays, direct counting on the specimens has been used with checking of radiographs for the larger specimens. It has not been found safe to depend on radiographs for the most posterior dorsal and anal rays as they are sometimes not visible in the radiograph.

TABLE III. Morphometric characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*. (Unless otherwise stated all percentages are of the head length.)

Item no.	Body part	*H. johnsonii*							*H. brevipes*		*H. affinis*			*H. johnsonii*		
		Günther, 1862 (holotype) Table I, No. 1		From Madeira Table I, No. 5 & 4 Author		From Cook Strait, N.Z. Table II, No. 5 & 6 Author		N.Z. Inst. Wellington Table II, No. 7, Author						From Grand Bank, Author		
		Günther (1862)	Author	(1)	(2)	(1)	(2)	(3)	Vaillant (1888)	Author	Collett (1905) Table I, No. 8 & 10 (5 syntypes)	Icelandic Slope Table II, No. 22, Author	Irish Atlantic Slope Table II, No. 15, Author	Table I, No. 29 (1)	Table I, No. 29 (2)	Table I, No. 28 (3)
1.	Total length, *mm*[a,b]	c	c	c	c	c	218	264	350	352[e]+	251–270	c	c	225	263	305
2.	Standard length, snout—end hypural, *mm*[a]	c	c	357	432	194	196	243	–	333	–	297	94	200	235.5	274
3.	Head length, *mm*[d,e]	61	60.9	90.5	103	45.2	46.7	57.5	89	83.2	61–64	70.8	24.6	50.0	57.9	64.8
4.	Snout, %[e]	A little >25	27	28	30	28[f]	27[f]	27	31	29[f]	ca.26	30	27	28	28	28
5.	Maxillary extension backward relative to eye, %[e]	$>\frac{1}{2}$	$\frac{3}{5}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{3}{7}$	Not $>\frac{1}{2}$	$\frac{1}{3}$	Almost $\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{3}$	$\frac{1}{2}$	$\frac{1}{3}$
6.	Lower jaw anterior relative to upper, *mm*[a,g]	0	1.5	0.7	1.7	1.8	1.9	2.3	Yes	1.8	Yes	1.0	1.0	1.3	1.4	2.0
7.	Eye diam (long), %[h]	ca.25	29	24	23	29[f]	30[f]	28	25	25[f]	26	25	31	27	27	26
8.	Interorbital space, %[i]	–	19	20	21	19	19	20	19	20	–	21	18	21	19	22
9.	Greatest height head, %[j]	>50	52	50	50	54	48	51	–	48	–	51	51	50	50	52
10.	Greatest width head, %[k]	–	42	42	50	41	41	39	–	45	47–54	43	43	49	48	49
11.	Greatest body height, %	–	71	75	74	ca.59	ca.50	ca.59	49	60	62–69	ca.65	66	69	71	63
12.	Height at origin 1st anal, %	–	56	64	61	46	ca.43	52	–	55	–	53	42	57	59	57
13.	Greatest body width, %[l]	44	33	44	49	21	20	31	44	39	–	36	29	41	40	40

14.	Width head as % height head	Much <100	81	84	100	76	85	76	A little >100	94	–	84	83	98	96	94
15.	Width body as % height body	–	46	59	66	36	c	53	89	65	–	55	44	59	56	63
16.	Greatest height body as % distance ant. margin orbit—end operculum	ca.100	98	103	103	79	c	82	–	85	–	89	91	96	100	87
17.	Snout—origin 1st dorsal, %[e]	110	114	113	114	115	114	112	–	112	–	120	116	117	117	117
18.	Snout—origin 2nd dorsal, %[e]	145	141	143	145	139	139	142	–	143	–	150	145	141	143	147
19.	Snout—anus, %[e,m]	179	188	202	213	200	190	197	–	194	–	204	182	196	192	204
20.	Ant. tip lower jaw—anus, %[e,m]	–	191	203	214	202	194	200	–	197	194–198	206	187	193	193	204
21.	Snout—origin 2nd anal, %[e,n]	276	266	285	301	285	291	286	–	282	–	295	270	278	278	287
22.	Base pelvic fin—anus, %[m]	ca.100	106	120	134	125	123	125	–	119	111–116	122	105	115	112	119
23.	1st dorsal origin behind vertical from base pectoral, %[o]	Immediately post.	8,3	14,9	17,13	15,11	11,9	11,9	Yes	12,8	Yes slightly	17,12	9,5	14,11	9,3	12,9
24.	Greatest height 1st dorsal to end of filament, %	ca.50	54	38	42	c	ca.39	50	–	c	ca.50[p]	c	49	58	47	c
25.	Length filament 1st dorsal beyond next longest ray, %	–	11	c	c	c	ca.10	10	–	c	ca.10[p]	c	c	20	5	c
26.	Length longest ray 2nd dorsal, %	A little <50	c	c	c	c	ca.42	38	–	c	–	c	c	46	36	43
27.	Pectoral length, %	>50	50+[e]	58+	59+	61+[e]	69	59	34	c	–	c	85	75	74	76
28.	Length longest ray pelvic, %	Outer ray produced to very fine filament of moderate length	c	49	51	c	ca.63	82	<17	c	–	c	c	76	64	c

(*Continued*)

TABLE III. Morphometric characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*. (Unless otherwise stated all percentages are of the head length.) — (*Concluded*)

Item no.	Body part	*H. johnsonii*							*H. brevipes*		*H. affinis*			*H. johnsonii*		
		Günther, 1862 (holotype) Table I, No. 1		From Madeira Table I, No. 5 & 4, Author		From Cook Strait, N.Z. Table II, No. 5 & 6 Author		N.Z. Inst. Wellington Table II, No. 7, Author	(holotype) Table I, No. 7					From Grand Bank, Author		
		Günther (1862)	Author	(1)	(2)	(1)	(2)	(3)	Vaillant (1888)	Author	Collett (1905) Table I, No. 8 & 10 (5 syntypes)	Icelandic Slope Table II, No. 22, Author	Irish Atlantic Slope Table II, No. 15, Author	Table I, No. 29 (1)	Table I, No. 29 (2)	Table I, No. 28 (3)
29.	Length filament pelvic beyond next longest ray, %	–	c	c	c	–	–	c	–	c	–	c	c	16	c	c
30.	Caudal fin, %[r]	Missing		c	c	c	43	c	26[c,q]?	c	31[p]	c	c	50[s]	48	48
31.	Length longest gill raker 1st branchial arch, %	–	11	9	10	13	13	13	–	12	–	13	14	16	16	13
32.	Length longest gill lamellae 1st branchial arch, %	–	6	7	7	5	5	5	–	7	–	7	7	7	6	6
33.	Anus below what ray 2nd dorsal	9	11	11–12	11	13	12	11	–	11	10–13	11–12	11	11	11	11
34.	1st anal below what ray 2nd dorsal	–	12	13	12–13	14–15	14–15	12	–	12	ca. 14	12–13	12	12	12	12

35. Condition when measured[t]

Very poor, from fish stomach, caudal missin[s]

Ex alcohol. Part of tail missing, also viscera, otherwise fair

Ex formalin. 1 day in water. Fair

Ex alcohol. Poor, body cavity empty

Ex alcohol. Fair but many fin rays broken and body cavity empty

Poor, unpaired fins, especially caudal strongly deteriorated

Ex alcohol. Body cavity slack and cut open. Tips of all fin rays broken off

Fair, fin rays usually broken off at tips

Ex alcohol. Rather poor, curved, fin rays broken

Ex alcohol. Moderately good except fin rays mainly broken and body cavity empty

Fair, ex 10% formalin

[a] In author's measurements, shortest distances between parallel planes through points named and perpendicular to the long axis of the fish.
[b] In author's measurements, greatest total length from tip of chin tubercle, with mouth closed, to posterior tip of caudal fin.
[c] Fin rays broken off so that true length is unknown, or otherwise unsuitable for this measurement.
[d] In author's measurements, snout—posterior end bony operculum.
[e] In author's measurements, with mouth closed and lower jaw fitting normally into upper.
[f] Average left and right.
[g] From tip of chin tubercle to symphysis of upper jaw, with mouth closed and lower jaw in normal position enclosed in upper jaw.
[h] In author's measurements, longitudinal diameter orbit.
[i] In author's measurements, least fleshy width.
[j] In author's measurements, from mandibular angle lower jaw.
[k] In author's measurements, over gill covers.
[l] In author's measurements, posterior to base of pectorals.
[m] In author's measurements, to mid anus.
[n] In author's measurements, beginning of 2nd anal is the anterior base of the first anal ray that has increased in size beyond the smallest ray which is defined as the posterior ray of 1st anal (Fig. 9).
[o] Shortest distances between verticals from anterior and posterior bases pectoral, respectively, to vertical to origin 1st dorsal.
[p] From Collett's (1905) figure of *H. affinis*.
[q] The query is Vaillant's as the caudal fin was evidently in too poor shape to determine its form, but judging from Vaillant's figure and the present condition of the specimen the caudal fin rays were broken off and the measurement probably included a greater length of caudal than to the mid line.
[r] In author's measurements, measured from the base of the mid line of the caudal fin.
[s] This specimen possessed longest rays in the central part of the caudal. Two other Grand Bank specimens had longer rays on either side of the mid line but those in the mid line may have been broken.
[t] In this species the skin is delicate and the general condition after preservation and some use always looks rather poor compared with a thicker-skinned species.

no standard lengths in his measurements of *H. affinis*. The tips of the caudal fin rays were definitely broken off in Vaillant's specimens of *H. brevipes* and the caudal fins of Collett's specimens of *H. affinis* may not have been perfect. Total length as a percentage of head length was 450–471 in the three Grand Bank specimens in which the caudal fin had approximately the correct length, only 411–428 in Collett's specimens of *H. affinis*, and 393 in Vaillant's *H. brevipes*. It has thus been necessary, in spite of the unsatisfactory nature of such comparisons, to make the main body-proportion calculations (Table III) on the basis of head length (H.L.) but, where possible, comparisons on the basis of the standard length (S.L.) have also been made (Table IV).

The head in Vaillant's specimen of *H. brevipes* is not in very good condition. The bones of the snout are broken transversely and the opercular bones are loose and not covered by the skin. The head may have dried out at some time. However, the condition is probably not so bad as to account for the difference between my measurement of 83.2 and Vaillant's of 89 mm for the head length. In my measurements the head length to the end of the bony operculum was 83.2 mm from the snout, and from the tip of the chin tubercle of the lower jaw: 86.5 mm with the mouth closed and the lower jaw normally fitting into the upper, 88.9 mm with the mouth slightly open and 89.8 mm with the mouth open a little more. Hence, it appears possible that Vaillant measured the head length from the anterior tip of the lower jaw rather than of the upper.

COMPARATIVE DESCRIPTIONS OF THE THREE NOMINAL SPECIES OF *HALARGYREUS* FROM THE NORTH ATLANTIC

General

All the *Halargyreus* examined in Tables II–IV possessed the following characteristics of the genus: the lower jaw extends beyond the upper; a tubercle is present on the lower jaw symphysis and points obliquely forward and downward; there are no teeth on the vomer and palatines; no barbel is present; the head is scaly to the snout tip; the operculum and suboperculum each terminate in a very small spine and both spines are close together; the anterior gill rakers of the 1st branchial arch are longer than the gill filaments; the caudal fin is separated from the dorsal and anal by a free peduncle; the 1st anal declines to and the 2nd anal increases from very short rays and the anals are continuous.

Halargyreus johnsonii

In the original description of *Harlargyreus johnsonii* Günther, 1862 and the subsequent examination of the holotype by the author at the British Museum (Fig. 1, Tables II–IV), the diagnosis is limited by the absence of the tail, with the break occurring anterior to the posterior parts of the 2nd dorsal and 2nd anal fins. The specimen also has a slack body cavity. Günther provided few reference data but my proportions for the type specimen are usually in fairly close agreement with his, considering the length of time in alcohol. In one regard there was complete disagreement, Günther stating

TABLE IV. Morphometric characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*. (All percentages are of the standard length, and all measurements are by the author, 1966–67.)

TABLE IV. Morphometric characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*. (All percentages are of the standard length, and all measurements are by the author, 1966–67.)

Item no.	Body part	*H. johnsonii* From Madeira Table I, No. 5 & 4 (1)	*H. johnsonii* From Madeira Table I, No. 5 & 4 (2)	*H. johnsonii* From Cook Strait, N.Z. Table II, No. 5 & 6 (1)	*H. johnsonii* From Cook Strait, N.Z. Table II, No. 5 & 6 (2)	*H. johnsonii* N.Z. Inst. Wellington Table II, No. 7 (3)	*H. brevipes* Table I, No. 7	*H. affinis* Icelandic Slope Table II, No. 22	*H. affinis* Irish Atlantic Slope Table II, No. 15	*H. johnsonii* Grand Bank Table I, No. 29 (1)	*H. johnsonii* Grand Bank Table I, No. 29 (2)	*H. johnsonii* Grand Bank Table I, No. 28 (3)
1.	Greatest total length, *mm*	[a]	[a]	[a]	218	264	[a]	[a]	[a]	225	263	305
2.	Standard length, snout — end hypural, *mm*	357	432	194	196	243	333	297	94	200	235.5	274
3.	Sex	F	F	–	–	–	F imm	F imm	–	M	M	F imm
4.	Head length, snout—end bony operculum, %	25.4	23.8	23.3	23.8	23.7	25.0	23.8	26.2	25.0	24.6	23.6
5.	Head length from tip chin tubercle with mouth closed, %	25.6	24.5	24.5	24.9	24.7	26.0	24.3	27.1	25.6	24.9	24.1
6.	Snout length with mouth closed, %	7.1	7.1	6.5[b]	6.5[b]	6.4	7.3[b]	7.2	7.0	7.1	6.8	6.7
7.	Lower jaw extension beyond upper, %[c]	0.2	0.4	0.9	1.0	0.9	0.5	0.3	1.1	0.7	0.6	0.7
8.	Post-orbital length — end bony operculum, %	12.3	11.5	10.2	10.3	10.5	11.5	11.4	11.0	11.3	10.9	10.9
9.	Orbit diam, longitudinal, %	6.1	5.4	6.7[b]	7.2[b]	6.6	6.1[b]	5.9	8.1	6.7	6.6	6.2
10.	Longitudinal diam cornea, %	5.0	4.6	[d]	[d]	[d]	[d]	[d]	[d]	5.5	5.4	–
11.	Interorbital space, least fleshy, %	5.1	5.1	4.4	4.6	4.7	4.9	4.9	4.8	5.2	4.7	5.2
12.	Snout with mouth closed — end maxillary, %	11.8	11.3	11.6	11.7	11.3	10.6	11.5	12.8	11.9	12.0	11.5
13.	Greatest height head, %[c]	12.6	12.0	12.6	11.4	12.1	12.0	12.2	13.4	12.4	12.3	12.3
14.	Greatest width head, %[c]	10.6	12.0	9.6	9.7	9.1	11.2	10.2	11.2	12.2	11.7	11.5
15.	Greatest height body, %	18.9	17.6	13.8	[d]	ca.14.0	14.9	15.5	17.2	17.2	17.5	14.9
16.	Height over mid anus, %	16.5	15.0	10.2	ca.10.0	11.8	13.8	12.0	11.0	14.0	13.6	14.0
17.	Height at origin 1st anal, %	16.1	14.5	10.7	ca.10.3	12.2	13.8	12.6	11.1	14.2	14.5	13.4
18.	Least height caudal peduncle, %	2.7	2.7	2.5	2.6	2.6	2.5	2.6	2.7	2.9	2.6	2.5
19.	Greatest width body, %[c]	11.2	11.7	4.9	4.8	7.4	9.7	8.5	7.6	10.2	9.9	9.3
20.	Snout — origin 1st dorsal, %[c]	28.6	27.2	26.9	27.1	26.5	28.0	28.7	30.3	29.3	28.8	27.7

(*Continued*)

TABLE IV. Morphometric characteristics of *Halargyreus johnsonii*, *H. brevipes*, and *H. affinis*. (All percentages are of the standard length, and all measurements are by the author, 1966–67.) — (*Concluded*)

Item no.	Body part	*H. johnsonii*						*H. affinis*		*H. johnsonii*		
		From Madeira Table I, No. 5 & 4		From Cook Strait, N.Z. Table II, No. 5 & 6		N.Z. Inst. Wellington Table II, No. 7	*H. brevipes* Table I, No. 7	Icelandic Slope Table II, No. 22	Irish Atlantic Slope Table II, No. 15	Grand Bank Table I, No. 29	Grand Bank Table I, No. 29	Grand Bank Table I, No. 28
		(1)	(2)	(1)	(2)	(3)				(1)	(2)	(3)
21.	Snout — origin 2nd dorsal, %[c]	36.1	34.6	32.4	33.2	33.6	35.8	35.8	37.9	35.2	35.1	34.7
22.	Snout — mid anus, %	51.3	50.7	46.6	45.2	46.5	48.6	48.6	47.6	48.9	47.3	48.1
23.	Ant. tip lower jaw with mouth closed — mid anus, %	51.4	51.0	47.2	46.1	47.3	49.3	49.1	48.8	49.9	48.2	49.1
24.	Snout — origin 2nd anal, %[c]	72.3	71.7	66.4	69.3	68.0	70.5	70.2	70.7	70.5	69.5	68.4
25.	Pelvic fin base — mid anus, %	30.5	32.0	29.2	29.4	29.5	29.8	29.1	27.4	28.8	27.5	28.1
26.	Greatest height 1st dorsal to end of filament, %	9.5	10.1	[a]	9.2	11.9	[a]	[a]	12.8	14.5	11.5	[a]
27.	Length filament 1st dorsal beyond next longest ray, %	[a]	[a]	[a]	2.3	2.3	[a]	[a]	[a]	5.0	1.3[e]	[a]
28.	Length longest ray 2nd dorsal, %	[a]	[a]	[a]	9.9	9.1	[a]	[a]	[a]	11.4	8.8	10.2
29.	Pectoral length, %	14.7+	14.0+	14.2[a]+	16.4	14.0	[a]	[a]	22.1	18.8	18.3	17.9
30.	Length longest ray pelvic, %	12.3	12.2	[a]	15.1	19.3	[a]	[a]	[a]	19.0	15.7	[a]
31.	Length longest gill raker 1st branchial arch, %	2.2	2.4	3.1	3.1	3.0	2.9	3.1	3.6	3.9	3.8	3.2
32.	Length longest gill lamellae 1st branchial arch, %	1.8	1.7	1.1	1.3	1.1	1.8	1.6	1.8	1.8	1.5	1.5

[a]Fin rays broken, unsuitable for measurement.
[b]Average left and right.
[c]Measurement taken as in Table III.
[d]Unsuitable for this measurement.
[e]Unable to determine whether or not filament was complete.

that the upper and lower jaws are equal in length anteriorly, whereas on examination it was found that with the mouth closed, and with the lower jaw fitting normally inside the upper, the lower jaw and especially the chin tubercle extended normally (for *Halargyreus*) beyond the upper jaw (Fig. 1, Table III, item 6). For the 1st anal, Günther says that the 4th–7th rays are the longest, decreasing in length to the 17th after which 4 or 5 short rays follow, preceding the stronger rays of the 2nd anal. My method of counting (Table II, footnote b, Fig. 9) included two of these intermediate fin rays with the 1st anal, or a total of 19.

The morphometric characteristics of the holotype of *H. johnsonii* agree fairly well with those of subsequent but considerably larger individuals of *Halargyreus* from Madeira (which are presumably *H. johnsonii*, being from the same locality, Fig. 2, Table III) if one allows for orbit diameter and gill-raker length values decreasing and some body height and width values increasing with increases in fish length, and some oblique measurement values increasing with increases in fish length, height, and width.

Halargyreus brevipes

Vaillant (1888) distinguished his new species *Halargyreus brevipes* (Fig. 3) from *H. johnsonii* in that in the latter: (*a*) the head is much higher than broad; (*b*) the maxillary passes the centre of the eye; (*c*) the jaws are equal in length anteriorly; (*d*) the dorsal begins at the level of the base of the pectorals; (*e*) the external ray of the pelvic is prolonged in a filament; and (*f*) the anterior gill rakers of the 1st branchial arch are longer than the branchial lamellae. He says that these characters of *H. johnsonii* are not found in *H. brevipes*.

Distinction (*a*) is not valid. The head width–head height ratio (Table III, item 14) does appear to be slightly greater in the single specimen of *H. brevipes* than in the holotype of *H. johnsonii*. This ratio, however, is at least as great in *H. johnsonii*, specimen No. 2 from Madeira, as in *H. brevipes*, and that for the latter is within the range of the head width–head height ratio of *H. johnsonii* from the Grand Bank.

Distinction (*b*) is valid for the two holotypes, with the backward extension of the maxilla in relation to the eye (orbit) in *H. brevipes* $\frac{1}{3}$ and that in *H. johnsonii* $\frac{3}{5}$. This ratio is, however, quite variable in *Halargyreus* and in related fishes and the difference between the holotypes is not sufficient for a species distinction. In our three specimens of *Halargyreus* from the Grand Bank (Table III) this character varies from $\frac{1}{3}$ to $\frac{1}{2}$. In the two additional *H. johnsonii* from Madeira the ratio is $\frac{1}{2}$ and in *H. johnsonii* from New Zealand it is $\frac{3}{7}$ to $\frac{1}{2}$ (Table III, item 5). In 11 specimens of the related *Lepidion lepidion* from the Grand Bank (author, unpublished) this character varied from $\frac{1}{4}$ to $\frac{2}{3}$, thus exceeding the *H. johnsonii* – *H. brevipes* – *H. affinis* range in both directions.

[a]Unable to determine whether or not filament was complete.

Distinction (*c*) is invalid as Günther's description was in error and the lower jaw of the holotype of *H. johnsonii* does protrude normally beyond the upper (Fig. 1, Table III, item 6).

Distinction (*d*) is invalid as Günther's statement is that the 1st dorsal origin is immediately posterior to the base of the pectoral and my observations show that in both species the dorsal is posterior to the verticals from the base of the pectoral. The dorsal is a little further posterior in *H. brevipes* than in the holotype of *H. johnsonii* but this characteristic for *H. brevipes* is within and for *H. johnsonii* within or close to the range of the specimens designated as *H. affinis*. Moreover, in the two recent specimens of *H. johnsonii* from Madeira the dorsal is further posterior, relative to the pectoral base, than in *H. brevipes* (Table III, item 23).

Distinction (*e*) is invalid in that all the long fin rays of *H. brevipes* are broken off and thus the long extension of the pelvic ray cannot be expected to be present. From Vaillant's measurements (Table III) and figure (Vaillant, 1888) it is evident that the fin rays were broken off at the time he observed and measured them.

Distinction (*f*) is invalid. My re-examination of Vaillant's holotype shows that as in *H. johnsonii* the longest anterior gill rakers of the 1st branchial arch in *H. brevipes* are distinctly longer than the branchial lamellae (Tables III and IV, items 31, 32).

In other characters of *H. johnsonii* (holotype) and *H. brevipes* the snout is a little shorter and the orbit a little longer in *H. johnsonii* but not beyond the bounds of probable variability within a species. Both of these measurements in *H. brevipes* are within the range of *H. affinis* and of the recent specimens of *H. johnsonii* from Madeira in percentages of head length (Table III, items 4 and 7), and close to or within the range of both these groups in terms of the standard length (Table IV, items 6 and 9). Greatest body height (Table III, item 11) was relatively very low in Vaillant's measurement and somewhat higher in my estimate of this measurement of *H. brevipes*. The specimen of *H. brevipes* is cut open down the middle of the ventral abdominal wall and the liver is absent. Thus the body cavity is empty and slack and accurate measurements of this character could not be made. The greatest body height and width have considerable variation in fishes. The greatest height of the body as a percentage of the standard length in 14 specimens of *Centrolophus niger* ranged from 25.7 to 30.6, and in 10 specimens of *Centrolophus britannicus* between 28.4 and 38.1. The range of greatest width of the body in seven specimens of *C. britannicus* was 5.7–11.2 (Templeman and Haedrich, 1966). Hence, for single specimens the relatively small differences in these proportions shown for *H. johnsonii* and *H. brevipes* have no specific significance. The distance from snout to anus (Table III, item 19), is a little shorter in the holotype of *H. johnsonii* than in that of *H. brevipes*, but it can be assumed that these small differences between individuals are within the normal range of variability of the species. For this character both of the present author's proportions for the holotypes *H.*

johnsonii and *H. brevipes* are included within the range of *H. affinis* and that of *H. brevipes* is included in the range of the three specimens of *H. johnsonii* from Madeira in terms of head length (Table III, item 19) and is less than the percentages for the two recent specimens in terms of standard length (Table IV, item 22). The absence of filaments on the 1st dorsal and pelvic and the short length of the pectoral and caudal fins in *H. brevipes* are of no significance since all long fin rays of the single individual of this species are and were broken off.

There is little difference in the few meristic characters which can be compared for *H. johnsonii* (holotype) and *H. brevipes*. Also for most meristic characters *H. brevipes* is within and in the remainder very close to the ranges of these characters for the four recent specimens of *H. johnsonii* from Madeira (Table II).

It is concluded, therefore, that for the characters examined there are no differences between *H. johnsonii* and *H. brevipes* from the North Atlantic which with the number and condition of specimens presently available can be considered to be of specific significance.

Halargyreus affinis

Collett (1904) distinguished his new species, *Halargyreus affinis* (Fig. 4, 5) from *H. johnsonii* by the longer lower jaw, projecting beyond the upper in the former, and the shorter head compared with the distance from the pelvic fins to the anus. The first distinction has been already shown to be invalid in that the lower jaw in both species projects approximately the same distance beyond the upper (Fig. 1–6; Table III, item 6). The distance from the base of the pelvic fin to the anus is shorter, 106% H.L. in the holotype of *H. johnsonii*, compared with Collett's 111–116% for *H. affinis*, but is within the range of this character in the new data for *H. affinis*, 105–122% H.L. Including the recent specimens of *H. johnsonii* from Madeira the range of this character in individuals from this area is even greater, 106–134% H.L., than for *H. affinis* and includes not only the range of Collett's *H. affinis* but that of all others except one (Table III, item 22).

The few meristic characters available for the holotype of *H. johnsonii* are within the range of those of *H. affinis*. Also, all meristic characters for the four recent specimens of *H. johnsonii* from Madeira (apart from the 2nd anal which overlaps in range and may be subject to minor errors of judgment) are within the range of these characters for *H. affinis* (Table II, Fig. 7–9).

Considering that head length, which varies considerably within a species, has been used as a base of comparison, and taking into account the previous discussion on the variability in width of head and in height and width of the body, the body proportions generally of *H. johnsonii* from the North Atlantic are close enough to those of *H. affinis* to be the same species (Table III).

Collett (1904) distinguished *H. affinis* from *H. brevipes* chiefly by the greater height of the body, and by the 1st dorsal and the pelvics of *H. affinis* being produced in a fine filament. Body height measurements are often highly

variable within species and as indicated in the previous discussion, *H. brevipes* is now in unsuitable condition for an accurate measurement of greatest body height. Judging by Vaillant's measurement it is apparent that the specimen was also, when measured by him, in no condition for an accurate measurement of body height. Our body height estimates, allowing for a full body cavity, (Table III, item 11) bring *H. brevipes* close to the lower range of Collett's measurements and of those of the Grand Bank specimens, and within the range of the latter on the basis of standard length (Table IV, item 15). In height over mid anus and height at the 1st anal, which are less susceptible to change with capture, preservation, and body condition (Table III, item 12; Table IV, items 16, 17), *H. brevipes* is within the range of *H. affinis* (including as *H. affinis* the Grand Bank *H. johnsonii*). Collett's second criterion of distinction has been shown to be invalid as all the long fin rays in *H. brevipes* are and were broken and consequently the presence or absence of filaments could not be demonstrated.

The remaining body proportions of *H. brevipes* not discussed above (Tables III, IV) were either within or close enough to the range of *H. affinis* that there could be no separation of the species on the basis of these proportions. This is especially true of the body proportions calculated as a percentage of standard length (Table IV) which for most morphometric characters is much preferable to head length as a basis for comparison.

All the meristic characters of *H. brevipes* (Table II), except the vertebral count, are within the range of those of *H. affinis*. The lower vertebral number of *H. brevipes* (51) compared with *H. affinis* (52–54) could be expected to occur as a normal variant in a larger number of *H. affinis* and especially in *H. affinis* of a much more southern and warmer area such as Morocco, the source of *H. brevipes*. In the 1st dorsal, *H. brevipes* has the usual (for *Halargyreus*) small anterior scale-like spine and 7 longer rays as described and illustrated by Collett (1905) for *H. affinis* (also see Fig. 7), instead of the 8 longer rays shown in Vaillant's (1888) figure. In actual count and from radiograph, the 2nd dorsal, the 1st anal, and total anal fin-ray numbers as taken by the author were less than those of Vaillant and fell into the normal range of *H. affinis*.

Usually for discrepancies in meristic counts, the new counts, using both fish and radiographs, are higher, but Vaillant's counts for the dorsal and anal rays are considerably higher than mine. I have checked carefully both on radiograph and on the actual specimen and there is no evidence that fin rays have been lost either anteriorly or posteriorly in these specimens. The 2nd–5th rays of the 2nd anal are absent but may be counted on the radiograph by the pterygiophores. Many fin rays of the dorsal and anal are broken and mostly split and separated into their left and right components. Some of these split rays may have entered Vaillant's counts as 2 rays. Vaillant's very high dorsal and anal counts would in any case be unlikely because of the very low vertebral count. (Note for example the New Zealand specimens in which high vertebral counts and also high dorsal and anal fin-ray counts are present.)

Conclusions Regarding the Name of the Species in the North Atlantic

On the evidence presented there is no reason to believe that *H. johnsonii*, *H. brevipes*, and *H. affinis* are not the same species. The differences between them are very minor and within the bounds of species variability. If subspecific or specific differences exist, more, and smaller, specimens from the southern area, the source of *H. johnsonii* and *H. brevipes*, are needed to establish them. Günther's (1862) *H. johnsonii*, lacking the posterior part of the tail and being imperfectly described, and Vaillant's (1888) *H. brevipes*, being in poor condition and imperfectly described, allowed Collett (1904), from more specimens in better condition, to describe the species a little more fully as *H. affinis* and to offer an excellent figure. All subsequent authors, except Maul (1952; Table I) for a specimen from Madeira, identified their individuals of this genus as *H. affinis*.

It is concluded that because a large part of an individual on which many measurements and other specific characters can be checked, and which is still in fair condition for examination, was described first by Günther (1862) and given the name *H. johnsonii*, this name has priority. Because the differences in characters of specific importance which served to separate *H. brevipes* and *H. affinis* from *H. johnsonii* and from each other have been demonstrated to be invalid, the latter two species names become junior synonyms of *Halargyreus johnsonii* Günther, 1862.

Halargyreus johnsonii from New Zealand

Three specimens of *Halargyreus* received at the British Museum (one from the New Zealand Institute, Wellington (undated) and two from Cook Strait, New Zealand, sent by the Colonial Museum, Wellington, and entered at the British Museum on December 13, 1873) were assigned to *H. johnsonii* by Günther (1887). Günther provided a few meristic characters (Table II) but no body proportions or figure as he considered the fish to be in too poor condition. I have recently examined these specimens from the British Museum (Fig. 6, Tables II–IV). They are in poor condition with regard to the measurements of the greatest depth of the body because the bellies are empty and flat, but the other measurements, especially anterior-posterior, should be moderately accurate.

Compared with counts for the North Atlantic *Halargyreus* (in parentheses) some of the meristic counts are higher for the New Zealand *Halargyreus* (Table II): for the 2nd dorsal, 56–58 (49–54); for the 1st anal 22–23 (19–22); for the 2nd anal 24–ca. 29 (21–26); for both anals 47–ca. 51 (41–47); and for the vertebrae 56–57 (51–54). The number of gill rakers on the 1st branchial arch is lower in the New Zealand specimens: 15 on the lower limb and total 20–21 (15–21 on the lower limb, total 21–28). The only complete meristic separation between these two populations of *Halargyreus* is thus in the 2nd dorsal and

in the vertebral counts. For *Halargyreus* these are related, the vertebral number being usually the same as, or one higher or lower than, the number of 2nd dorsal rays.

Günther's counts for the dorsal and anal of the New Zealand specimens are low, sometimes much lower than mine for apparently the same fish.

In body proportions (Tables III, IV) the New Zealand *Halargyreus* are toward the highest point of the range for orbit length but the flesh around the orbits is shrunken from long preservation in alcohol or drying out and the orbit is occasionally distorted so that these orbital lengths are maximal. The greatest body height is rather low but the specimens are in poor shape for an accurate measurement of this character. The heights at the mid anus and at the beginning of the 1st anal which are more reliable, because the shape is less distorted in this region, overlap the lower part of the range of the North Atlantic *Halargyreus*. The greatest body width in two of the New Zealand specimens is extremely low, 20–21% H.L., 4.8–4.9% S.L., compared with a range for the North Atlantic specimens of 29–49% and 7.6–11.7% respectively. In the third New Zealand specimen the greatest body width at 31% H.L. is within the North Atlantic *Halargyreus* range and at 7.4% S.L. very close to the lower part of this range.

The considerably greater width of the head than of the body in two of these New Zealand *Halargyreus* compared with North Atlantic specimens (Fig. 6B, Tables III and IV) indicates that the body width is unnaturally low in these New Zealand specimens. It is possible that the New Zealand specimens were abnormally present in shallow water and that their feeding may have been prevented or interfered with for a long time before capture. Thus the thinness of the specimens and especially of two of them may be abnormal and the greatest height, in this case, would be reduced also.

In the remaining body proportions the ranges of the New Zealand specimens are within, overlapping, or close to those of the North Atlantic specimens. Fin-ray and fin measurements and especially those to the tip of filaments of these and all other *Halargyreus* specimens are usually minimal because it is often impossible to be certain whether a fin tip and especially a very fine filamentous ending of a fin ray is broken or not.

The main differences between *H. johnsonii* from New Zealand and from the North Atlantic are in meristic characters and in body width and height. All of these are susceptible to environmental influences. Although recognizing the possibility of specific or subspecific differences, it is best at this time, pending the examination of more New Zealand or other southern ocean specimens in good condition, together with information on water temperatures, salinities, oxygen, etc. in their normal abode, to continue to recognize the species as *H. johnsonii*.

DISTRIBUTION

The main centres of abundance of *H. johnsonii* in the North Atlantic, on the basis of present records, are from south and west of Iceland to the

FIG. 1. Lateral view of head region of *H. johnsonii* (holotype), head length 61 mm, Table I, No. 1.

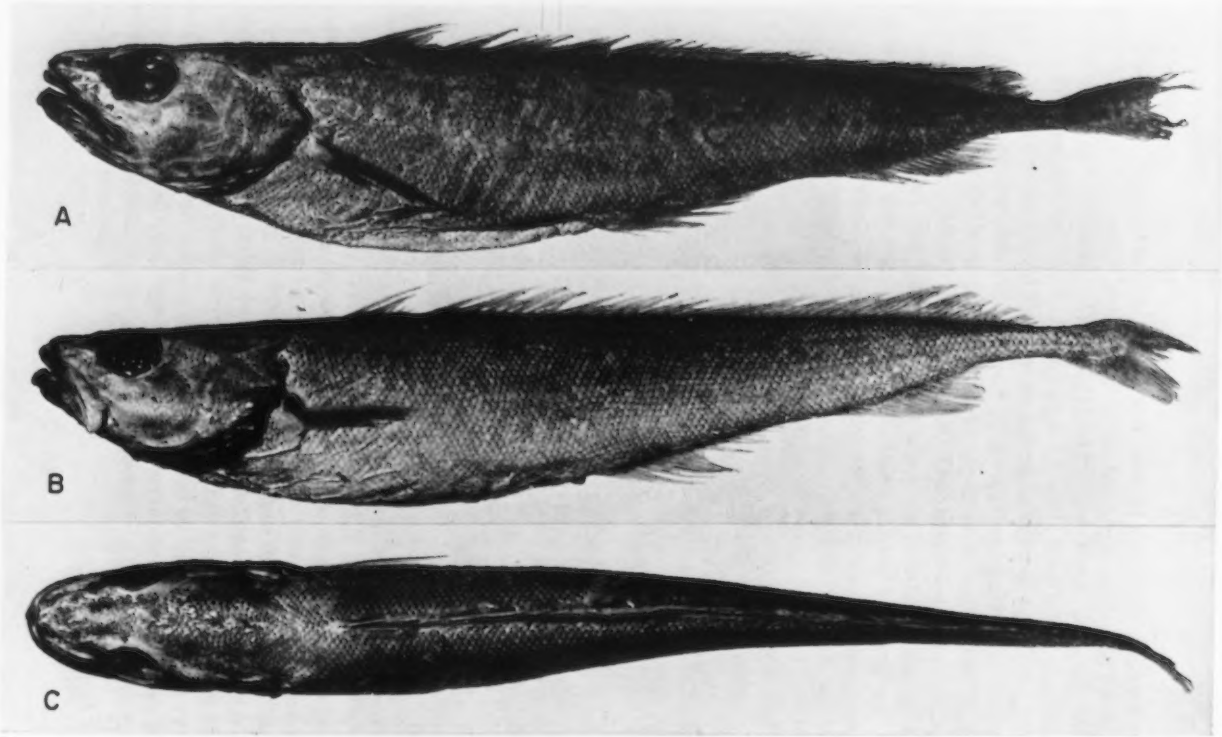

FIG. 2. Lateral views A and B, and dorsal view C, of *H. johnsonii* from Madeira: A and C, standard length 432 mm, Table I, No. 4; B, standard length 357 mm, Table I, No. 5.

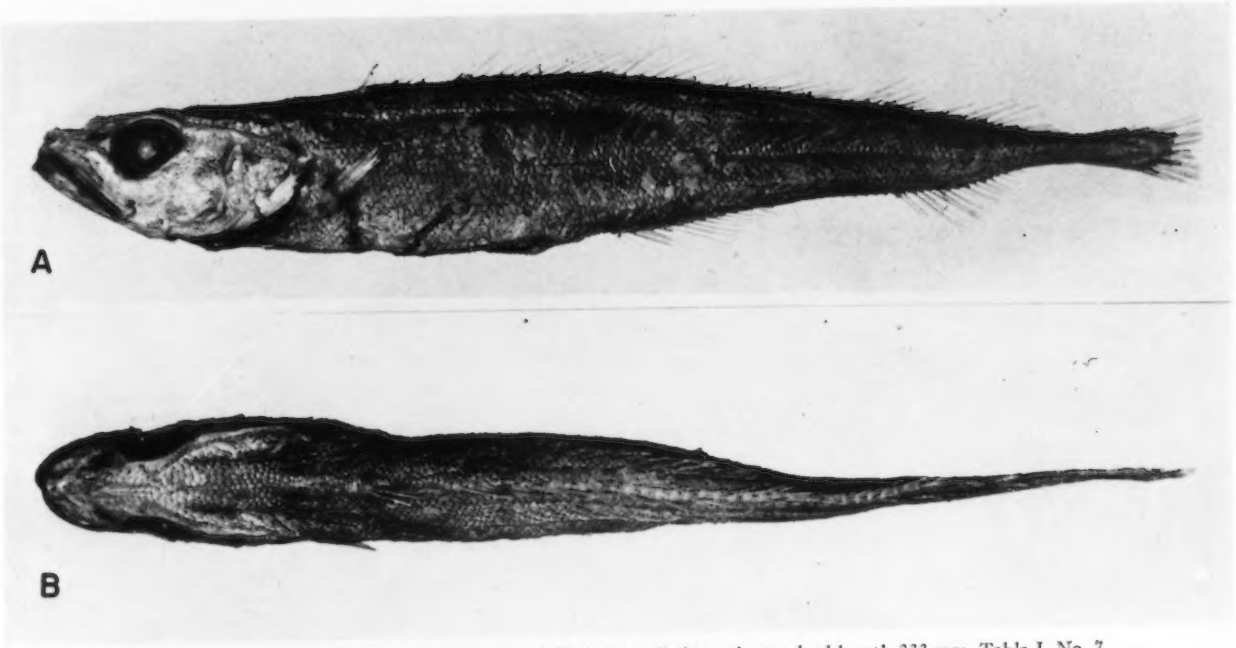

FIG. 3. Lateral view A, and dorsal view B, of *H. brevipes* (holotype), standard length 333 mm, Table I, No. 7.

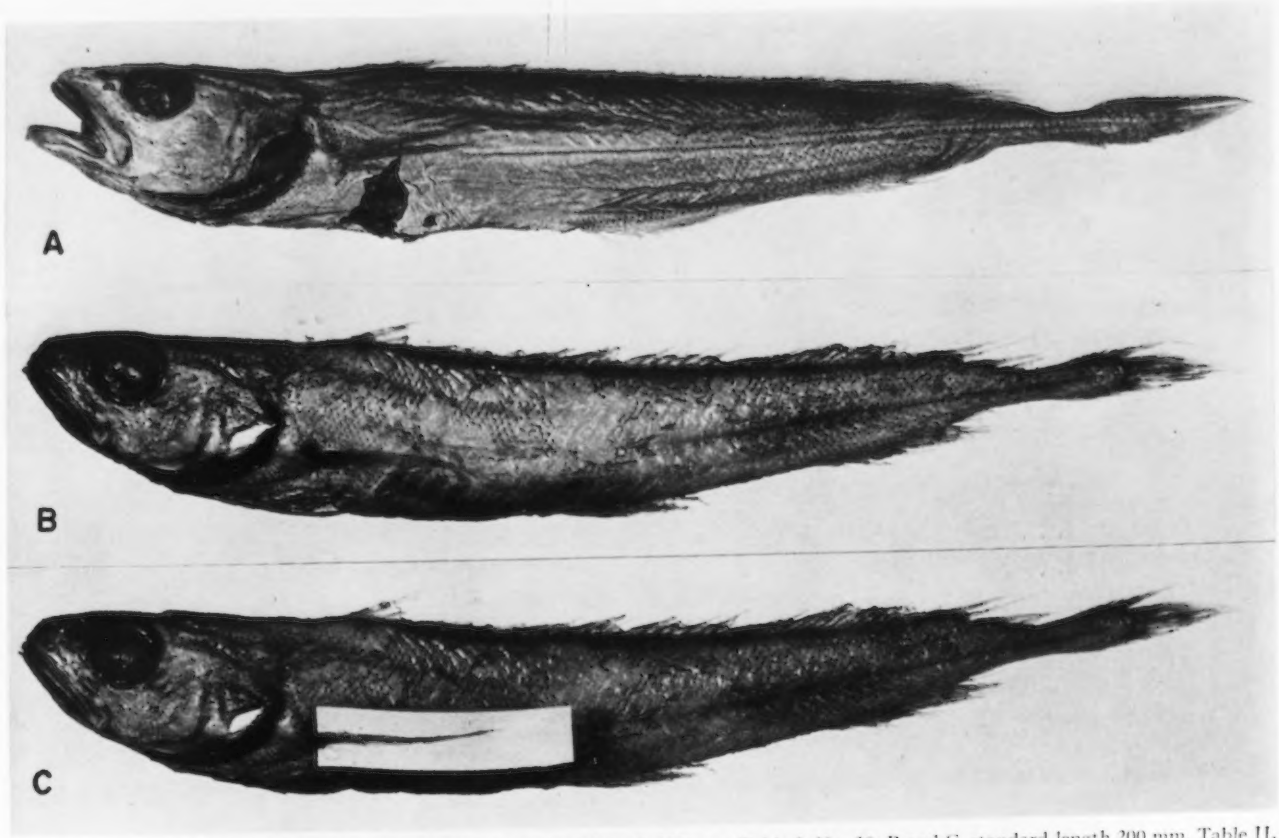

FIG. 4. *Halargyreus johnsonii* from the Grand Bank: A, standard length 274 mm, Table I, No. 28; B and C, standard length 200 mm, Table II, No. 24.

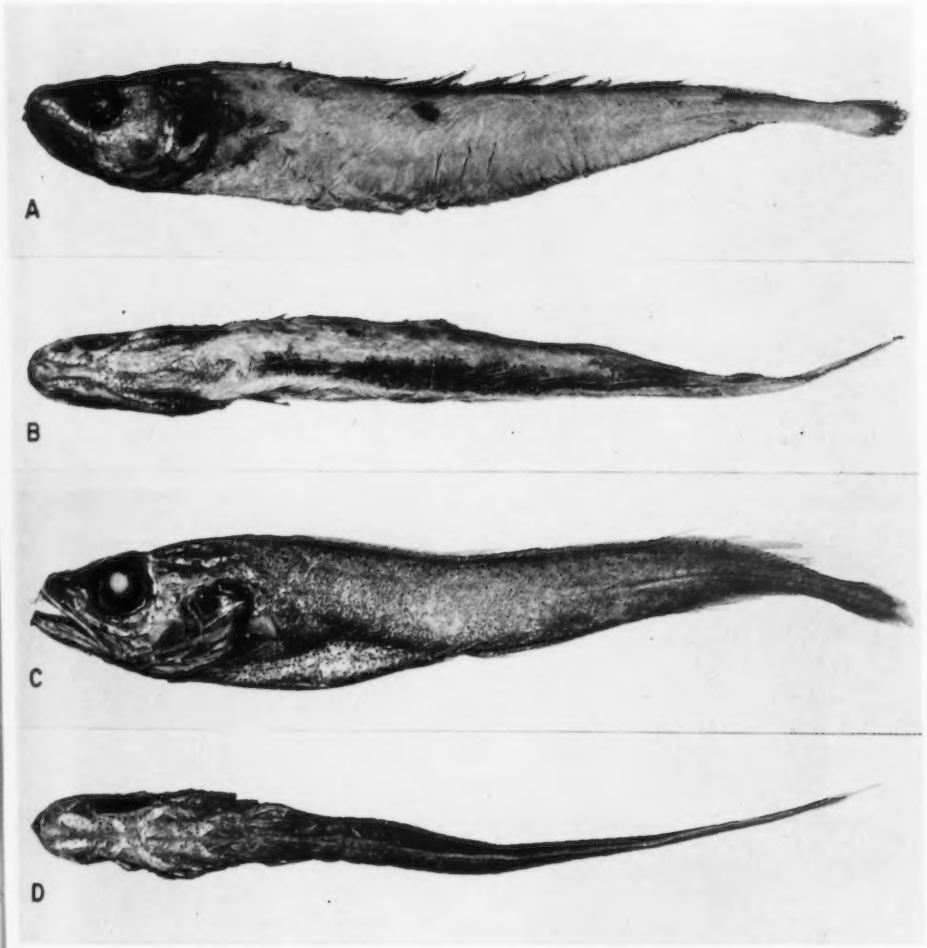

FIG. 5. Lateral view A, and dorsal view B, of specimens reported as *H. affinis* from west Icelandic Slope, standard length 297 mm, Table II, No. 22; and from the Irish Atlantic Slope, lateral view C, standard length 94 mm, Table II, No. 15, and dorsal view D, standard length 110 mm, Table II, No. 42.

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FIG. 4. *Halargyreus johnsonii* from the Grand Bank: A, standard length 274 mm, Table I, No. 28; B and C, standard length 240 mm, Table II, No. 24.

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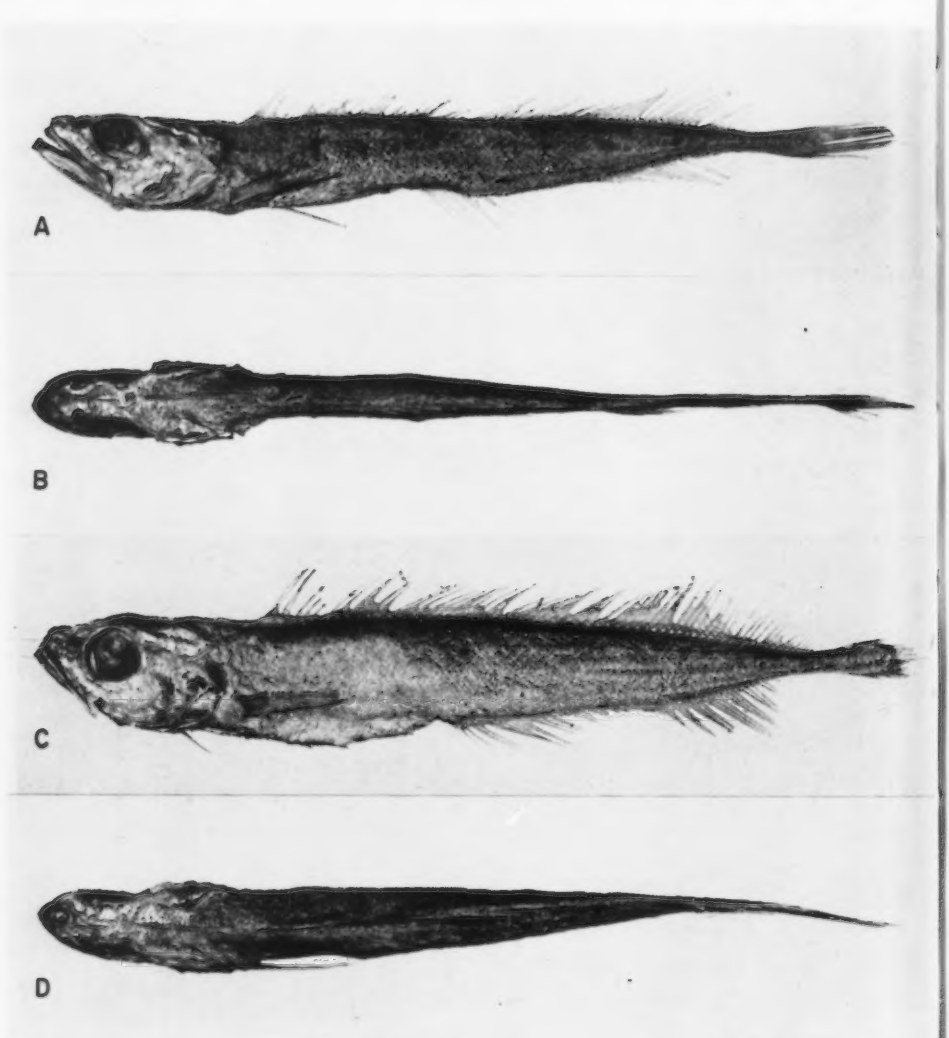

FIG. 6. Lateral view A, and dorsal view B, of *H. johnsonii* from Cook Strait, New Zealand, standard length 196 mm, Table II, No. 6 (author); and lateral view C, and dorsal view D, of *H. johnsonii* from the New Zealand Institute, Wellington, standard length 243 mm, Table II, No. 7 (author).

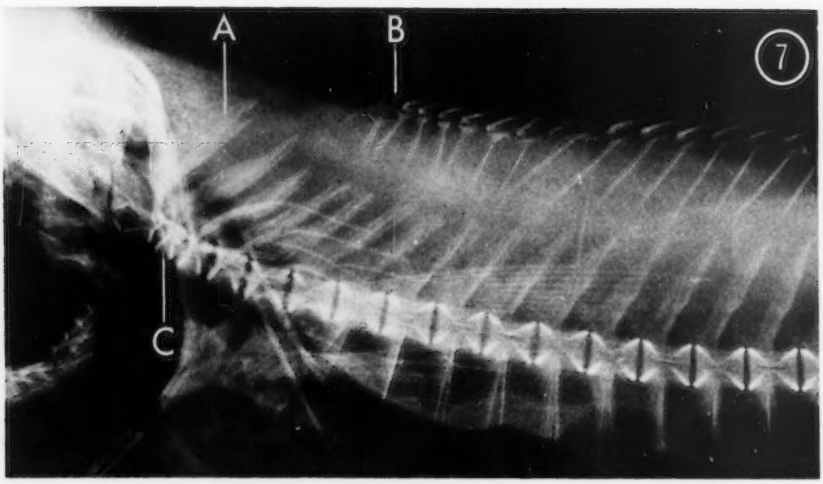

FIG. 7. Radiograph of lateral view of antero-dorsal portion of *H. johnsonii* from Madeira, standard length 317 mm, Table II, No. 2: A, 1st neural spine, broader, especially dorsally, than those immediately posterior; B, rudimentary spine at anterior base of 1st dorsal; C, 2nd centrum of vertebral column, the smallest centrum of the anterior region. (Note also the 7 long rays of the 1st dorsal and the beginning of the long rays of the 2nd dorsal.)

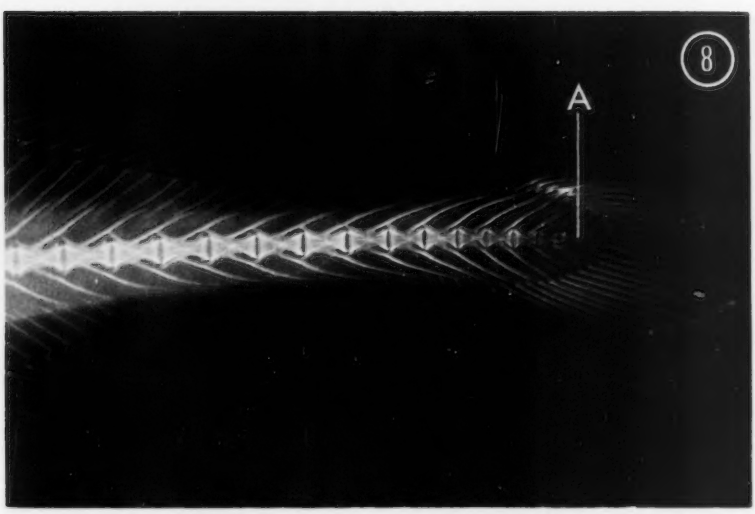

FIG. 8. Radiograph of lateral view of posterior part of *H. johnsonii* from Madeira, standard length 406 mm, Table II, No. 4A: A, hypural, the most posterior segment counted in the vertebral column. (Note also the posterior rays of the 2nd dorsal and of the anal and the free portion of the caudal peduncle.)

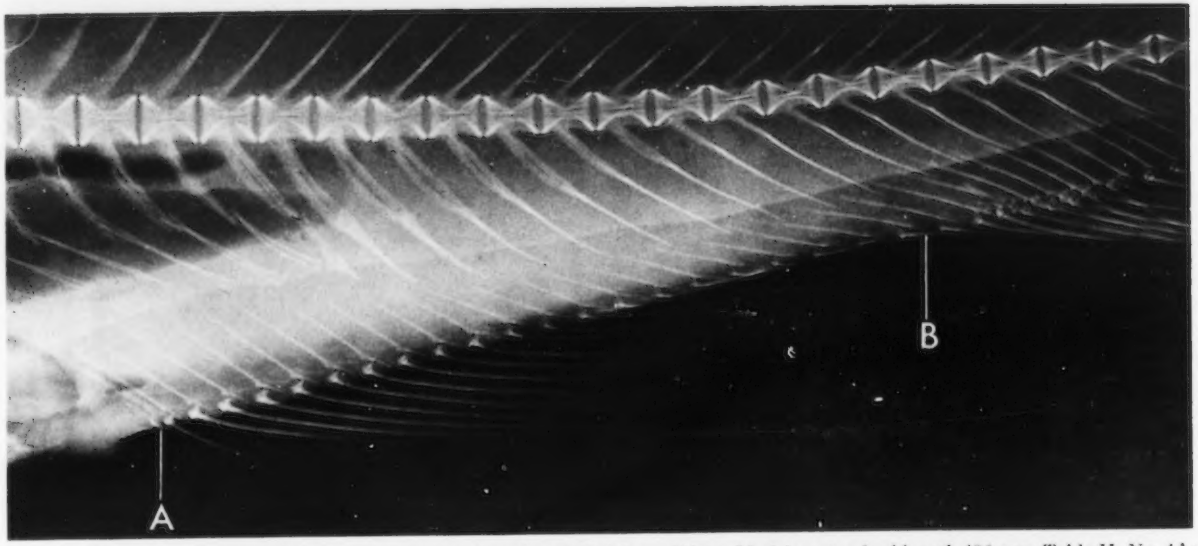

FIG. 9. Radiograph of lateral view of postero-ventral portion of *H. johnsonii* from Madeira, standard length 406 mm, Table II, No. 4A: A, 1st ray of 1st anal; B, 1st ray of 2nd anal.

Faroes Shelf and west of Ireland. There is a considerable gap between the centre of relative abundance west of Ireland and the most southerly records to the east — the six specimens of *H. johnsonii* from Madeira and the type specimen formerly called *H. brevipes* off Morocco (Fig. 10, Table I). Compared with its relative abundance in the north-central and northeast Atlantic *H. johnsonii* is rather scarce in the western Atlantic, only three

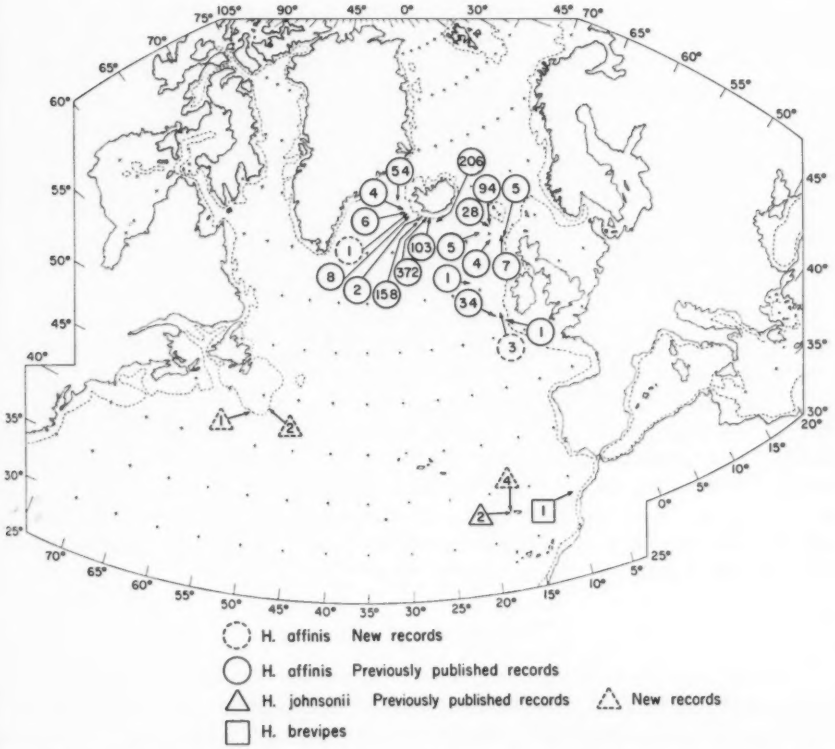

FIG. 10. Distribution of reported captures in the North Atlantic of *H. johnsonii* and of the nominal species *H. affinis* and *H. brevipes* (now all *H. johnsonii*.) (Numbers refer to the number of specimens captured — see Table I. The map used for this figure was adapted from an outline chart of the North Atlantic Ocean on an azimuthal equal area projection centered at 40°N, 35°W, prepared at the Woods Hole Oceanographical Institution by M. J. Pollack and G. G. Pasley, April 1951. The 100-fath (183-m) isobath is shown.)

having been noticed in our hauls, although for many years sets have been made routinely on redfish cruises as deeply as 730 m and always with the codend lined with mesh small enough to retain *Halargyreus* over 10–15 cm. However, two of the three Grand Bank specimens were taken in a single trawl haul so that they may not be strays in the western Atlantic but not readily

available to trawls because of their generally pelagic or deeper distribution. Günther (1887) says that numerous examples of this species appeared some years ago on the coast of New Zealand. Three of these were sent to the British Museum and were examined by Günther and by the author (Tables II–IV). Dr Daniel M. Cohen informs me that new specimens of *Halargyreus* have now been taken off New Zealand and off South America and that he will be reporting on them.

The account of the earlier New Zealand captures indicates that they were shallow and if so were probably due to some underwater disturbance of the school which led them into shallow water where being not at home they were readily captured or drifted ashore.

In the Atlantic it is a deep-living species and the anterior projection of its lower jaw indicates that it is probably a pelagic feeder. In the northeast Atlantic (Table I) captures have ranged between 350 (pelagic over 1319) and 1061–1256 m, and bottom temperatures of 5.19–10.23 C. The greatest numbers have been taken at depths between 700 and 841 m and bottom temperatures of 5.19–ca. 7.0 C. On the Grand Bank the specimens were taken between 585 and 785 m and at bottom temperatures of 3.81–4.11 C.

Since the recent German captures of 103–372 *H. johnsonii* in four sets on the south Icelandic Slope (Table I) it is evident that this fish must be abundant in certain areas of the north-central Atlantic.

Other than the records of Table I and Fig. 10, the only additional reference we have found to *Halargyreus* from the North Atlantic and Mediterranean areas is that of Grey (1956) who says that Edgerton (1955) photographed a fish (in the deep water of the Mediterranean) that he called *Halargyreus*, but which was probably *Lepidion lepidion*. Actually, Edgerton did not mention *Halargyreus* but named the fish, shown in two photographs, *Haloporphyrus* (= *Lepidion*) which it apparently is.

FOOD

There appears to be no published information available on the food of *Halargyreus*. In all three Grand Bank specimens and in all the other specimens examined by the author the stomach was everted and forced into the mouth cavity. Also Collett (1905) says regarding his specimens (of *H. affinis*) that the stomach was forced into and filled the mouth cavity and was empty.

A 1-cm long portion of the posterior part of the intestine of specimen No. 20 (Table II) from the Icelandic Slope contained parts of a small and a medium-sized specimen of the pelagic shrimp *Pasiphaea*, probably *P. tarda*.

COLOUR

Günther (1862) says that the colour of *H. johnsonii* appears to have been a delicate red on silvery ground with pectoral and anal transparent and the mouth and gill cavity black.

Vaillant (1888) for *H. brevipes* gives the colour as reddish, silvery on the jaws and ventrally, pectorals dark, buccal and branchial cavities an intense black.

Collett (1905) for *H. affinis* says that the colour cannot be stated but it appears to have been light red grey. The abdomen and the sides of the head are silvery.

Maul (1952) says that the colour, on his formalin specimen, was brown on the body and head, and lighter below, with the dorsal, anal, and pectorals brown, the anal and pelvics whitish, and the inside of mouth, branchiostegal membranes, and iris blackish.

In the Grand Bank specimen first examined for colour 5 years after capture and preservation in formalin the colour was whitish grey, and silvery below. In the other two specimens after 2 years in formalin the general colour is brownish grey but this is merely the flesh colour showing through the translucent greyish skin. In the two more recent specimens the colour is more silvery along the belly and the lower part of the jaws. Scales are absent in both so that the true colour is unknown. Mouth and branchial cavities and peritoneum are black.

At the present time after long immersion in alcohol the general body colour of Vaillant's *H. brevipes* is light brown, and along the sides of the head, silvery. The general colour of the New Zealand specimens of *H. johnsonii* is silvery, due to the appearance of the skin. Blacker's specimens from the *Ernest Holt*, captured in 1960 and preserved at the British Museum in alcohol, are now silvery brownish above and on the tail and silvery on the sides of the head and on the belly.

Two large specimens from Madeira are greyish brown above and lighter, brownish grey below on the belly in the specimen with the colour best preserved.

Size and Maturity

The largest *Halargyreus* specimen reported up to the present time (Table I, II) is 432 mm S.L. from Madeira. The largest in the more northerly parts of the eastern Atlantic is 340 mm total length from the Icelandic Slope, and the largest from the western Atlantic, 274 mm S.L.

No fresh weights are available. The weights of two of the largest specimens available to us, from Madeira, out of 10% formalin and soaking in water for 3 hr, were 381 g for the fish of 357 mm S.L. and 630 g for that of 432 mm S.L. The latter is the largest specimen known.

The testes of all four males examined between 211 and 274 mm S.L. were small and there was no superficial evidence of maturity. In females the observations on maturity are given below (ovary weights are estimated and egg diameters measured; Imm. = immature):

S.L. (*mm*)	Ovary weight (g)	Egg diam (*mm*)	Maturity	Locality	Captured on
218	0.1	–	Imm.	Icelandic Slope	Mar. 18
249	0.2	–	Imm.	Icelandic Slope	Mar. 18
274	–	<0.1	Imm.	Grand Bank	May 5
297	0.4	–	Imm.	Icelandic Slope	Mar. 18
317	0.9	<0.1	Imm.	Madeira	–
333	1.5	–	Imm.	Morocco	–
357	4	0.1	Imm. or imm. condition	Madeira	June 17
406	5	0.13	Imm. or imm. condition	"	Aug. 14
432	6	0.3	Imm. or imm. condition	"	May 24

The eggs were translucent except for the largest fish which had a few small, 0.3-mm diam, opaque yolky eggs, and the second largest in which the eggs, though tiny, were somewhat opaque. None of the fish showed any indications of having spawned previously, although the largest was presumably maturing. It is therefore likely that considerably larger individuals of this species exist, possibly in very deep water where they may be taken on longlines or in more efficient trawls than have hitherto been used at these depths.

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REFERENCES

BLACKER, R. W. 1962. Rare fishes from the Atlantic slope fishing grounds. Ann. Mag. Nat. Hist., Ser. 13, **5**: 261–271.

COLLETT, R. 1904. Diagnoses of four hitherto undescribed fishes from the depths south of the Faroe Islands. Forh. Vidensk. Selsk. Christiania, 1904, No. 9. 7 p.
1905. Fiske, indsamlede under "Michael Sars" togter i Nordhavet 1900–1902. Rept. Norwegian Fish. Marine Invest., **2**(2): 1–151.

EDGERTON, H. E. 1955. Photographing the sea's dark underworld. Natl. Geograph. Mag., **107**: 523–537.

GREY, MARION. 1956. The distribution of fishes found below a depth of 2000 metres. Chicago Nat. Hist. Museum, Fieldiana: Zool., **36**(2): 73–337.

GÜNTHER, ALBERT. 1862. Catalogue of the fishes in the British Museum. Vol. 4. London. p. 1–534.
1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873–1876. Challenger Rept., **22**(Zool.): 1–268.

HJORT, JOHAN. 1909. Review of Norwegian fishery and marine investigations 1900–1908. Plan and organisation of the work. Rept. Norwegian Fish. Marine Invest., **2**(1): 7–67.

HOLT, E.W.L., AND L. W. BYRNE. 1908. Second report on the fishes of the Irish Atlantic slope. Sci. Invest. Fish. Ireland, 1906, **5**: 1–63.

HUBBS, CARL L., AND KARL F. LAGLER. 1958. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci., No. 26. 213 p.

KOEFOED, EINAR. 1927. Fishes of the sea-bottom. Rept. Sci. Res. Michael Sars Atlantic Deep-Sea Expedition 1910. p. 1–148.

KREFFT, G. 1965. Rare fish (distant northern seas) Germany. Conseil Perm. Intern. Exploration Mer, Ann. Biol., **20**: 108.
1966. German observations of rare fish in 1964. Distant northern seas. Ibid., **21**: 175–178.
1967. German observations of rare fish in 1965. Ibid., **22**: 183–186.

MAUL, G. E. 1952. Monografia dos peixes do Museu Municipal do Funchal, Familia Gadidae e Bregmacerotidae. Bol. Museu Municipal Funchal, **6**(15): 5–51.

TEMPLEMAN, WILFRED, AND RICHARD L. HAEDRICH. 1966. Distributions and comparisons of *Centrolophus niger* (Gmelin) and *Centrolophus britannicus* Günther (Centrolophidae) from the North Atlantic. J. Fish. Res. Bd. Canada, **23**(8): 1161–1185.

VAILLANT, L. 1888. Expéditions scientifiques du "Travailleur" et du "Talisman" pendant les années 1880–1881–1882–1883. Poissons. Paris. 406 p.

Food and Feeding Habits of Swordfish, *Xiphias gladius*, in the Western North Atlantic[1]

By W. B. Scott

Royal Ontario Museum, Toronto, Ont.

AND

S. N. Tibbo

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

In the northern part of its western Atlantic range, the swordfish feeds on relatively few species of fish. Volumetrically the most important species are Atlantic mackerel, barracudinas, silver hake, redfish, and Atlantic herring. Squid are also important in the diet, and accounted for nearly one-fifth of the volume in the stomachs examined. There is evidence that the swordfish frequently uses its sword to attack and disable even small individual food items before ingesting them.

INTRODUCTION

This is a report on stomach contents of about 500 swordfish taken by commercial and research vessels in the Northwest Atlantic. Until 1962 the commercial catch of swordfish in the Northwest Atlantic was taken almost exclusively by harpoons. Since then, longlining has become increasingly important and harpooned fish now constitute only a small proportion of the total catch. Knowledge of food and feeding habits is useful for capturing most species of fish regardless of the fishing method but is of special significance when success depends on the use of bait.

The large size of swordfish and the fact that they are dressed at sea as soon as possible after boating, make difficult the collection of quantitative data on their food. Certainly, the food and feeding habits of swordfish are less well known than are those of most other commercial fishes.

MATERIALS AND METHODS

This study is based on an examination of 514 swordfish stomachs collected on 13 cruises during the years 1958–1965 (Fig. 1 and Table I). For samples 1–10 (taken aboard commercial vessels) food items were identified to species, if possible, otherwise to genus or family, and the number in each taxon was counted. Samples 11 and 13 were taken during cruises of the research vessel

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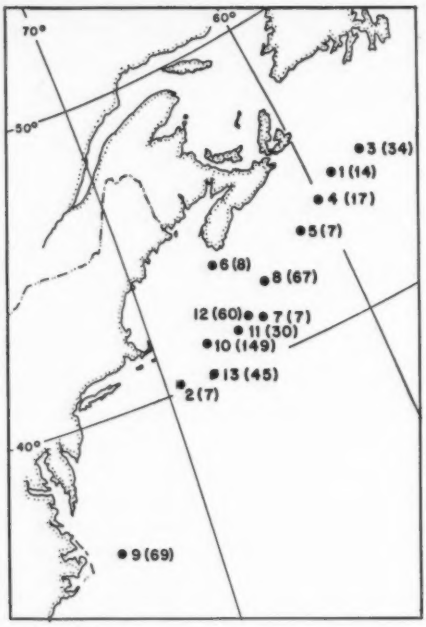

FIG. 1. Distribution of swordfish stomach samples. Number of stomachs examined shown in brackets after sample numbers.

A. T. Cameron. Sample 12, although taken during a cruise of a commercial vessel (the *Alder Point*), was carefully preserved at sea and the contents treated volumetrically at the Royal Ontario Museum.

Samples 1–7 were first reported on by Tibbo et al. (1961). These data were re-examined in an attempt to assess the relative importance of various fish species and also of fish vs. squid in the swordfish diet.

Volumetric analyses were attempted only on samples 11, 12, and 13. Whenever practicable the amounts of fish and squid were measured separately; however, when digestion was far advanced, the separation of the individual items was not attempted.

In the northern portion of its western Atlantic range, the swordfish is caught mainly during summer months. Thus, 9 of the 13 samples were taken during July and August; 3 were collected in September and October (Table I). Sample 9 is unique since it was taken in March, and is the most southerly sample.

STOMACH CONTENTS

FISHES

In all, 31 species or species groups were represented in the samples (Table II). The prey species may be divided arbitrarily into three groups based on

TABLE I. Dates of collections, locations, and numbers of swordfish stomachs examined.

Sample no.	Date	Location	No. of stomachs
	1958		
1	July 25–28	44°N; 59°W (Banquereau and Sable Is. banks)	14
	1959		
2	June 22–July 5	40°N; 69°30′W (S of Nantucket Shoals)	7
3	Aug. 9–22	44°30′N; 56°50′W	34
4	July 9–14	43°30′N; 62°W (S of Sable Is. Bank)	17
5	July 18–19	42°55′N; 61°30′W	7
6	Sept. 1–4	Browns Bank	8
7	July 15–30	41°N; 66°W (Corsair Canyon to Middle Ground)	7
	1963		
8	July 3–18	41–43°N; 62–66°W	67
	1964		
9	Mar. 4–28	35°30′–36°00′N; 74°30′–75°W	69
10	July 6–19	40°N; 67°W	149
11	Aug. 1–15	40–42°N; 65–67°W	30
12	Oct. 4–16	40°30′N; 66°15′W	60
	1965		
13	Sept. 27–Oct. 3	40°20′N; 67°45′W–41°25′N; 66°15′W	45
Total			514

the number of samples in which they were found. The first group, consisting of four species or species groups (silver hake, barracudinas, redfish, and lanternfishes) occurred in a minimum of nine samples and would appear to be of primary importance. The second group of six species occurred in 4–6 of the 13 samples and may be considered of secondary importance. Of lesser importance is the third group, consisting of 21 species that appeared in only one or two samples. Table II also shows that the number of species recorded from the various samples varied from 5 to 18, the northernmost samples containing the least number of prey species. Sample 9, the most southerly sample, contained 18 species, 9 of which appeared in no other sample. None of the four species in the first group, and only three of the second group occurred in sample 9.

Generally, these data suggest that in the northern part of its range the swordfish feeds on fewer, but more abundant, species than in the southern part. This is not an unexpected situation, since there are fewer species off the Canadian coastline than there are off the Atlantic coast of Florida, for example. At least 1000 marine species occur in Florida waters (Briggs, 1958), whereas only 300 species occur off the Atlantic coast of Canada (Leim and Scott, 1966).

TABLE II. Fish species recorded from stomachs, and their distribution on basis of numbers of samples in which they were found.

Prey species or group	Sample no.												
	1	2	3	4	5	6	7	8	10	11	12	13	9[a]
Merluccius bilinearis	x	x	x	x	x	x	x	x	x	x	x	x	
Paralepididae	x	x	x	x			x	x	x	x	x	x	
Sebastes marinus	x		x	x	x		x	x	x	x	x		
Myctophidae	x	x	x	x			x	x	x		x	x	
Clupea harengus						x	x	x	x		x	x	
Scomber scombrus									x	x	x	x	x
Alepisaurus spp.		x							x		x	x	x
Argentina silus	x		x	x				x					
Chauliodus spp.									x	x	x		x
Scomberesox saurus					x			x			x	x	
Ammodytes spp.											x		x
Poronotus triacanthus									x				x
Petromyzon marinus											x		x
Anguilliformes											x		x
Selar crumenophthalmus											x		x
Gempylidae											x		x
Sphyrna sp.													x
Squalus acanthias													x
Stomias boa		x											
Gadus morhua													x
Melanogrammus aeglefinus					x								
Pollachius virens					x								
Urophycis sp.										x			
Nezumia bairdi											x		
Centropristes striatus													x
Stenotomus chrysops													x
Palinurichthys perciformis													x
Prionotus sp.													x
Echeneidae													x
Monacanthidae												x	
Lophius americanus													x
Total species in sample	5	5	5	5	5	2	5	7	9	6	15	8	18

[a]Sample 9 listed last because of its southerly position and the exceptional number of prey species that were recorded.

Volumetrically the most important species are mackerel, barracudina, silver hake, redfish, and herring (Table III). The lanternfishes (Myctophidae), which rank fourth in Table II, are in 10th position in Table III, and contributed only 162 cc for the three samples. The lanternfishes, thus, are of less significance than their frequency of occurrence would suggest.

A discussion of the 31 species of fishes or species groups listed in Tables II and III follows. The order of treatment follows Table III as far as possible.

TABLE III. Frequencies and volumes of fish species or groups occurring in three samples having a total of 135 stomachs. Numbers of stomachs in samples in parentheses.

Species or group	Sample 11 (30)			Sample 12 (60)			Sample 13 (45)			Total volume (*cc*)
	Occurrence	T.I.[a]	Volume (*cc*)	Occurrence	T.I.	Volume (*cc*)	Occurrence	T.I.	Volume (*cc*)	
Mackerel, *Scomber scombrus*	16	18	4,116	34	45	9,630	27	30	4,325	18,071
Barracudinas — Paralepididae	1	11	750	10	157	4,015	15	39	5,165	9,930
Silver hake, *Merluccius bilinearis*	2	22	2,273	8	35	4,600	4	4	1,200	8,073
Redfish, *Sebastes marinus*	1	2	1,364	3	4	2,165				3,529
Herring, *Clupea harengus*				2	27	2,355	2	2	800	3,155
Saury, *Scomberesox saurus*				1	6	620	2	2	145	765
Hake, *Urophycis* sp.	1	3	682							682
Snake mackerels — Gempylidae				4	17	435				435
Filefishes — Monacanthidae							4	8	320	320
Lanternfishes — Myctophidae				1	14	90	5	5	72	162
Lancetfishes, *Alepisaurus* spp.				3	3	145	1	1	9	154
Bigeye scad, *Selar crumenophthalmus*				3	3	95				95
Sand lances, *Ammodytes* spp.				1	16	80				80
Viperfishes, *Chauliodus* spp.	1	1	10	1	8	65				75
Marlin-spike, *Nezumia bairdi*				1	1	45				45
Eels — Anguilliformes				2	14	25				25
Unidentified fishes	12	38	2,264	49	586	9,570	10		2,405	14,239
Totals			11,459			33,935			14,441	59,835

[a]T.I. = Total individuals.

Atlantic mackerel, *Scomber scombrus*.— The role of mackerel in the swordfish diet is problematical because it is frequently used as bait, and was so used in each of the three samples for which volumes of stomach contents are available. Volumetrically it ranks first in importance by a considerable margin. The 18,071 cc total for the three samples is almost double the 9930 cc total for barracudinas. However, mackerel occurred in only 5 of the 13 samples and in 4 of these mackerel was used as bait. In sample 12, 34 of the 60 stomachs examined contained mackerel, sometimes 2, 3, or even 4 in a stomach.

Although not all mackerel showed hook marks, there can be no doubt that some of those ingested were bait, since hook marks were clearly visible. In some cases, the advanced state of digestion prevented positive designation as bait. Since individual stomachs contained 2, 3, or 4 mackerel, it may be that swordfish "collect" the bait from the hooks before being hooked. In any case the data suggest that mackerel is a good bait for swordfish longlining.

Barracudinas (Paralepididae).— The barracudinas are important food items both in terms of frequency of occurrence and by volume. They occurred in the greatest number in a single stomach, for 80 specimens (210–250 mm total length) were counted in the stomach of a 65-inch (fork length) swordfish taken in sample 12. These 80 fish occupied 825 cc. Ingested barracudinas were frequently slashed and the fragile bodies formed a mass that was often reported by technicians aboard commercial vessels as "unidentified fish remains." Because of the identification problem, it is probable that the proportion of barracudinas in the diet is even higher than indicated by our figures.

Barracudinas are primarily bathypelagic fishes. The white barracudina, *Notolepis rissoi*, the most common species in the study area, occurs at depths of 100–200 m and deeper. These fishes have been observed to swim vertically, in a snout-up or snout-down position (Houot, 1958; Rofen, 1966), a behavioural characteristic that would seem to make them particularly susceptible to the slashing attack of the swordfish.

Silver hake, *Merluccius bilinearis*.— Silver hake occurred in all except the most southerly sample (sample 9), to a maximum of 22 individuals in a single stomach (sample 4). It occurred in more samples than any other species and ranked third in volume.

Since silver hake are seldom, if ever, used for bait, this species must constitute a most important food item. It is of interest that few silver hake exhibited slash marks.

Only Tibbo et al. (1961) and Bigelow and Schroeder (1953) have previously reported silver hake in swordfish stomachs, although Goode and Gill (1887) did report "whiting," probably in reference to this species.

Best available evidence indicates that silver hake live near bottom; sometimes, especially at night, they may rise off bottom. We presume that hake are eaten when they are off bottom.

Redfish, *Sebastes marinus*.— Redfish were found in 9 of the 13 samples, ranking third in importance of occurrence (Table II) and fourth in volume (Table III). However, they occurred in only 4 stomachs of the 135 making up samples 11, 12, and 13. Usually, only one or two individuals were found in a single stomach but eight redfish were eaten by one swordfish in sample 1.

We conclude that swordfish eat redfish more or less incidentally and that, because of their large size, redfish constitute an appreciable volumetric component in the diet.

Atlantic herring, *Clupea harengus*.— Comparable perhaps to the redfish, herring appeared to be eaten more or less incidentally by swordfish. However, they may be taken in large numbers, up to 30 in a single stomach as in sample 6. Of the 135 stomachs in samples 11, 12, and 13 (Table III) only 4 (less than 3%) contained herring. One stomach in sample 12 contained 24 herring; significantly, not one of these showed external evidence of slashing.

These data suggest that individual swordfish may feed heavily on herring when a school is encountered.

Note that the volumes of individual species (or families) of prey fishes listed below herring in Table III decrease abruptly. The total volume for herring was 3155 cc, for the saury 765 cc. Thus, the first five species listed in Table III are of primary importance, whereas the remaining species are of less significance, and are treated in less detail below.

The saury, *Scomberesox saurus*, occurred in only three stomachs in the volumetric samples (11, 12, 13), and in four of the 13 samples. As many as 12 sauries occurred in a single stomach in sample 6. However, sauries appear to be only an occasional food item.

Hake, *Urophycis* sp., (probably *U. tenuis*), was recorded from only a single stomach (three individuals) and must be considered a rare food item.

The snake mackerels (Gempylidae), although probably not a major food item, are none the less of great interest. Four stomachs in sample 12 contained a total of 17 gempylids in various stages of digestion. Most showed evidence of slashing. Sometimes the anterior portion of the head, clearly severed from the rest of the head, was all that remained in the stomach. These fish were provisionally identified as *Nealotus tripes* Johnson, according to the information presented by Grey (1953). The recent report of this species in the Canadian Atlantic by Beckett and Barrett (1967) tends to substantiate this identification.

Filefishes (Monacanthidae) were recorded only from four stomachs in sample 13. These shallow-water fishes are an occasional prey.

Lanternfishes (Myctophidae) may be eaten in large numbers (51 individuals in a stomach in sample 7) but, because of their relatively small size, they are not significant volumetrically. They are frequently either decapitated or slashed. Unfortunately, our data do not permit us to say which species occurred with greatest frequency. Some individuals were identified to the

genus *Myctophum* and others to the species *Aethoprora metopoclampa* (Cocco), *Lampadena speculigera* Goode and Bean, *Taaningichthys minimus* Tåning, and *Notoscopelus krøyeri* (Malm).

The lancetfishes, *Alepisaurus* spp., are eaten occasionally, seldom more than one per stomach, usually with the head severed and the body in several pieces. Existing evidence suggests that *Alepisaurus* spp. inhabit the upper layers of the ocean (Gibbs and Wilimovsky, 1966). Two species have been reported from the North Atlantic (Gibbs, 1960) but specific determinations of ingested specimens were not possible.

The bigeye scad, *Selar crumenophthalmus*, occurred in two samples only and is considered an occasional prey. Three stomachs in sample 12 each contained a single scad.

The sand lances, *Ammodytes* spp., also appeared only in two samples and should be considered as occasional prey. The one swordfish in sample 12 that ate sand lances had 16 individuals in the stomach.

Viperfishes, *Chauliodus* spp., appeared in four samples (Table II), more frequently than might be expected of a moderately deepwater species. One stomach in sample 12 contained eight specimens, all with heads severed, presumably slashed. Viperfishes were probably classed as "unidentified" in the earlier samples and may thus be eaten more frequently than the record indicates. The viperfishes are considered to inhabit mid depths, extending from surface layers (0–50 m) at night to 500–2000 m by day. Haffner (1952) notes, that of the two North Atlantic species of *Chauliodus*, *C. sloani* has the narrower vertical distribution (1000–1800 m by day, 0–800 m by night). It is unfortunate that specific identification of ingested *Chauliodus* was not possible, for knowledge of the species consumed might provide a better appreciation of the depths at which swordfish feed.

The marlin spike, *Nezumia bairdi*, occurred only once, as a single specimen in sample 12.

Eels (Anguilliformes) appeared in only two samples. Fourteen eels, in an advanced state of digestion, occurred in two stomachs in sample 12; more exact identification to species was not attempted.

Comparison of Fish vs. Squid in Stomachs

Examination of stomach contents indicated that during the periods of study (March–October) swordfish fed on the short-finned squid, *Illex illecebrosus*, as well as on numerous fish species. Of the 514 stomachs examined, 94% contained fish and only 61.5% contained squid; 47% contained fish and squid together; 36% of the total sample contained fish only; and 5.4% contained squid only (Table IV).

In this qualitative analysis no record of the actual quantities of these two food items is available, but the data suggest that fish was a more important food item than squid.

A volumetric analysis for comparison of these two food items in samples 11–13 was attempted (Tables V–VII). In all cases fish occurred in significantly

greater quantities than squid. The average quantities for each of fish and squid were:

	Fish	Squid
Sample 11	381.9 cc	187.3 cc
Sample 12	565.5	91.0
Sample 13	320.9	64.3

TABLE IV. Incidence of fish and squid in each of 13 samples and percentage incidence of each food item.

Date	Sample no.	No. of stomachs	Fish	Squid	Fish and squid[a]	Fish only	Squid only
1958							
July	1	14	14	7	7	7	
1959							
June & July	2	7	7	7	7	–	
August	3	34	34	12	12	22	
July	4	17	17	6	6	11	
July	5	7	7	3	3	4	
September	6	8	8	4	4	4	
July	7	7	7	2	2	5	
1963							
July	8	67	61	30	25	36	6
1964							
March	9	69	59	35	26	32	9
July	10	149	142	111	104	38	7
August	11	30	27	29	26	1	3
October	12	60	59	49	0	11	1
1965							
Sept.–Oct.	13	45	40	21	19	14	2
Total		514	482	316	241	185	28
Percentage			94	61.5	47	36	5.4

[a]Identified only as inseparable fish and squid.

When the volumes of the three samples, totalling 135 stomachs, were summed, squid accounted for only 16% of the volume, whereas fish made up 78%, almost five times as much as squid:

Sample	No. of stomachs	Volume			
		Fish	Squid	Fish and squid	Total
11	30	11,459 cc	3,935 cc	1,372 cc	16,766 cc
12	60	33,935	5,462	–	39,397
13	45	14,441	2,895	3,160	20,496
Total	135	59,835	12,292	4,532	76,659
Percentage		78.0	16.0	6.0	

TABLE V. Volumes (cc) of fish, squid, and contents identified only as inseparable fish and squid, in each of the 30 stomachs in sample 11.

Stomach no.	Fork length (*cm*)	Fish	Squid	Fish and squid	Total volume
1	121.0	270	180	–	450
2	122.3	–	15	–	15
3	130.2	–	5	–	5
4	139.8	–	–	125	125
5	141.5	–	–	60	60
6	141.8	25	495	–	520
7	142.5	175	85	45	305
8	147.3	235	10	–	245
9	153.0	–	–	100	100
10	153.3	2,160	125	–	2,285
11	155.8	315	85	–	400
12	156.1	20	175	–	195
13	157.8	1,080	690	–	1,770
14	161.8	250	–	45	295
15	162.7	350	10	–	360
16	163.1	150	–	85	235
17	163.6	315	–	–	315
18	167.4	325	40	–	365
19	168.5	250	290	–	540
20	169.7	120	–	110	230
21	166.9	90	30	–	120
22	171.3	300	–	55	355
23	176.0	–	30	–	30
24	176.6	2,408	150	–	2,558
25	179.4	215	5	–	220
26	179.4	1,666	–	682	2,348
27	184.2	300	75	–	375
28	187.0	365	100	45	510
29	193.7	75	925	–	1,000
30	209.0	–	415	20	435
Totals		11,459	3,935	1,372	16,766
Avg		381.9	187.3	58.2	558.9
Percentage		68.4	23.4	8.2	100.0

OTHER FOOD ITEMS

In addition to various species of fishes and the short-finned squid, other items appeared in the stomachs from time to time, although never in sufficient numbers to be considered a significant food item.

Evidence that the swordfish occasionally eats large squid of the suborder Oegopsida was apparent from large squid jaws, or beaks (Fig. 2) found in stomachs. On a few occasions squid of the genus *Ommastrephes* were so identified. At times whole specimens were recovered, although in an advanced state of digestion.

The cephalothorax of the shrimp *Acanthephyra purpurea* was removed from a stomach in sample 12 taken off Georges Bank. The specimen was retained by Dr Bousfield of the National Museum of Canada, who informed us that this species occurs at depths of 100–3000 fath in the North Atlantic.

The euphausiid *Meganyctiphanes norvegica* was encountered on a few occasions but not in large numbers.

Occasionally specimens of the small octopus *Bathypolypus arcticus* occurred in the stomachs, usually not more than one per stomach.

Relationship between Swordfish Size and Volume of Contents

In an effort to determine if our data indicated a relationship between size of swordfish and volumes of stomach contents, scatter diagrams were prepared using the data of Tables V, VI, and VII. A general trend of greater volumes in larger fish was evident in the diagrams but was not clearcut, perhaps a reflection of regurgitation after capture, as noted by Tibbo et al. (1961).

USE OF THE SWORD

There is a special appeal in studies of food and food-getting among the swordfish and spearfishes because of the unique spear-like rostral development and its use as a slashing instrument to maim or injure smaller fishes upon which they feed. The swordfish differs from the spearfishes (marlins and sailfishes) in that the sword is long and is dorso-ventrally compressed (hence, the name broadbill), whereas the spearfishes have a shorter spear and it is slightly compressed laterally. Thus, the swordfish appears to be more highly specialized for lateral slashing. Such a specialization would seem to be pointless unless directed towards a vertically oriented prey, or unless the swordfish slashes mainly while vertically oriented, as when ascending or descending.

The food items in samples 11, 12, and 13 were examined for evidence of slashing. The results are inconsistent, the percentage of stomachs showing evidence that the contents had been slashed varying from 10% in sample 11 to 53% in sample 12:

Sample	No. stomachs	No. slashed	Percentage
11	30	3	10
12	60	32	53
13	45	13	29

These figures show little except that the per cent of slashing may be relatively high in a collection of stomachs. A stomach may have contained a slashed barracudina and a whole mackerel but would be considered as providing evidence of slashing.

No consistent pattern was evident. No one species was always slashed or not slashed. Mackerel were often found to be cut into two or three pieces, but equally often were whole. It does seem worthy of note that of the 24 herring in a stomach in sample 12 not one showed evidence of slashing.

TABLE VI. Volumes (cc) of fish and squid in each of the 60 stomachs in sample 12.

Stomach no.	Fork length (*cm*)	Fish	Squid	Total volume
1	102.9	280	–	280
2	115.6	130	5	135
3	116.2	–	20	20
4	119.4	35	25	60
5	123.8	265	60	325
6	125.7	55	15	70
7	133.3	180	50	230
8	137.2	340	55	395
9	137.2	110	35	145
10	137.8	140	–	140
11	137.8	780	80	860
12	138.4	170	90	260
13	139.1	320	140	460
14	139.1	325	175	500
15	139.7	195	605	800
16	139.7	35	70	105
17	139.7	115	140	255
18	141.0	300	5	305
19	141.6	340	4	344
20	142.2	300	290	590
21	144.8	345	3	348
22	144.8	160	–	160
23	146.0	595	70	665
24	146.0	1,678	3	1,681
25	146.7	210	1	211
26	149.9	20	145	165
27	149.9	1,572	20	1,592
28	151.8	430	35	465
29	152.4	275	160	435
30	152.4	2,020	30	2,050
31	154.3	120	180	300
32	154.3	380	935	1,315
33	157.5	320	1	321
34	157.5	325	225	550
35	158.7	785	–	785
36	160.0	265	–	265
37	160.0	760	–	760
38	161.3	285	270	555
39	163.2	475	20	495
40	165.1	825	215	1,040
41	165.7	90	–	90
42	167.6	1,365	270	1,635
43	167.6	820	10	830
44	169.5	35	35	70
45	175.3	740	–	740
46	177.2	715	1	716
47	180.3	680	25	705
48	182.9	400	3	403
49	185.4	1,390	35	1,425
50	185.4	415	5	420
51	186.7	440	–	440
52	187.3	995	1	996
53	187.3	1,220	160	1,380
54	187.9	1,370	110	1,480
55	187.9	1,000	490	1,490
56	191.8	1,915	–	1,915
57	191.8	1,610	105	1,715
58	199.4	155	–	155
59	213.4	1,685	30	1,715
60	215.9	635	5	640
Totals		33,935	5,462	39,397
Avg		565.5	91.0	656.6
Percentage		86.2	13.8	

TABLE VII. Volumes (cc) of fish, squid, and contents identified only as inseparable fish and squid, in each of the 45 stomachs in sample 13.

Stomach no.	Fork length (*cm*)	Fish	Squid	Fish and squid	Total volume
1	74.1	–	–	20	20
2	91.5	40	–	–	40
3	93.6	710	–	–	710
4	95.5	30	60	–	90
5	96.1	350	–	10	360
6	100.1	40	–	30	70
7	103.6	90	20	–	110
8	105.0	30	–	–	30
9	109.9	50	–	–	50
10	113.0	40	–	60	100
11	113.3	450	–	–	450
12	114.4	–	–	50	50
13	114.7	120	100	80	300
14	115.4	200	–	–	200
15	115.5	90	–	30	120
16	115.5	280	–	–	280
17	119.2	230	130	30	390
18	120.5	100	–	–	100
19	121.6	80	20	80	180
20	126.0	299	220	140	659
21	128.0	360	–	270	630
22	128.0	680	–	–	680
23	128.2	400	–	–	400
24	134.9	133	–	350	483
25	135.0	–	20	–	20
26	135.9	240	–	110	350
27	139.5	230	10	–	240
28	142.0	90	60	180	330
29	145.5	730	130	420	1,280
30	151.5	–	70	–	70
31	155.2	700	560	–	1,260
32	163.1	360	–	–	360
33	166.8	–	–	360	360
34	167.3	1,080	–	–	1,080
35	167.8	975	90	–	1,065
36	173.6	600	145	80	825
37	175.5	84	10	–	94
38	176.8	1,620	150	–	1,770
39	179.5	–	490	110	600
40	190.1	730	–	–	730
41	190.6	300	220	360	880
42	192.1	80	220	–	300
43	193.5	100	120	390	610
44	199.0	730	–	–	730
45	215.7	990	50	–	1,040
Totals		14,441	2,895	3,160	20,496
Avg		320.9	64.3	70.2	455.4
Percentage		70.5	14.1	15.4	100.0

It may not be sufficient, however, to look only for obvious cuts or decapitation as evidence of slashing. The use of X-rays (Fig. 3) indicated that, although external evidence may be absent, the prey may still have a separated vertebral column. In this specimen, a gempylid *Nealotus tripes*, the break in the tissue above the fractured vertebral column took place after preservation in formalin.

The fact that so many fishes removed from stomachs were slashed immediately behind the head (mackerel, white hake, and even the small lanternfishes) suggested that they were sought out and struck individually, rather than as victims of a slashing attack on a school.

The large numbers of slashed barracudinas found in the stomachs of swordfish may be significant, particularly in the light of the suggestions by Houot (1958) and Rofen (1966) that these fishes swim in a vertical plane.

Bait experiments, using marked or stained baits, and baits of different shapes suspended in a variety of ways from hooks, might yield worthwhile information on swordfish feeding habits.

DISCUSSION

A number of authors have contributed to knowledge of the food and feeding habits of the swordfish, although only small numbers of swordfish were examined and these were taken at the surface by harpooning.

One of the earliest observers, Clark (1886), remarked that in the Gulf of Maine swordfish fed chiefly on dogfish, mackerel, and herring and that the principal food "...in the past season" south of Cape Cod had been squid and skipjack. Goode and Gill (1887) noted that swordfish fed "...on menhaden, mackerel, bonitos, bluefish" and also herring. These authors also quote a fishing captain who said that swordfish "...feed on mackerel, herring, whiting and menhaden."

Kingsley (1922) noted the presence of lanternfishes (Myctophidae) in swordfish stomachs and speculated that since they were in such good condition, the swordfish must "...make a rapid transition from the feeding grounds to the surface for the after dinner siesta."

Parr (1933) described as new a species of stomiatid fish from a swordfish stomach; this was subsequently re-identified as *Stomias boa*. In the same publication Parr reported the first western Atlantic specimen of a deepwater stomiatoid fish, *Trigonolampa miriceps* Regan and Trewavas, from the stomach of a swordfish caught on Georges Bank. To this day only four specimens of this species have been reported.

Gregory and Conrad (1937) wrote that "The swordfish follow the mackerel northward in July and August. Our own party, however, did not find mackerel remains in their stomachs." This is a strange statement considering the lack of evidence.

Bigelow and Schroeder (1953), in discussing food of swordfish, list mackerel, menhaden, bluefish, silver hake, butterfish, herring, argentines, and rattails, and mention also squid and giant squid (perhaps *Architeuthis* sp.).

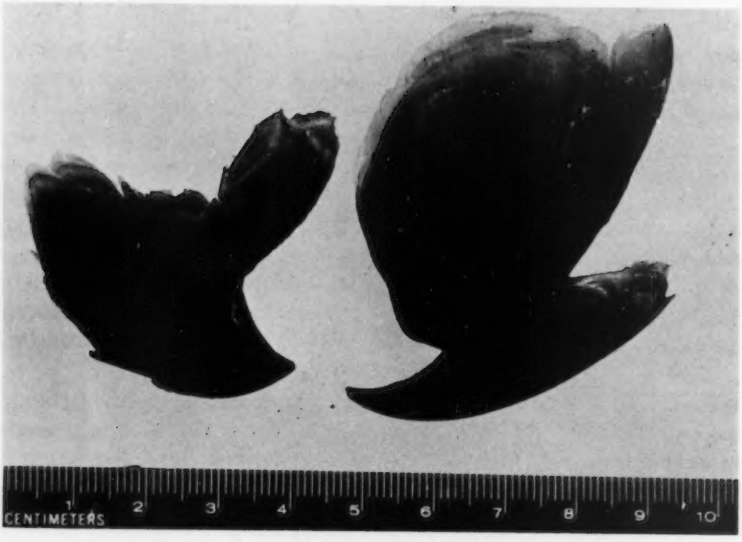

FIG. 2. Beaks from squid of sub-order Oegopsida.

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FIG. 3. X-ray photograph of a gempylid, *Nealotus tripes*, from a swordfish stomach. Note the dislocated vertebral column.

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These authors also noted that the late Walter H. Rich of the U.S. Bureau of Fisheries had reported the following genera in swordfish stomachs taken off Georges and Browns banks: *Alepisaurus*, *Chauliodus*, *Lampadena*, *Macrostoma*, *Myctophum*, *Notoscopelus*, and *Stomias*.

Arata (1954) reported on stomach contents of small swordfish (6.1–192.1 mm standard length) and found that identifiable fishes were mainly surface forms, such as scombrids (mackerel-like fishes), exocoetids (flyingfishes), xiphiids (swordfish), and istiophorids (spearfishes).

Scott and Crossman (1959) reported a snake-eel, *Omochelys cruentifer*, that had been attached to the stomach lining of a swordfish caught off Cape Breton, N.S.

Yabe et al. (1959), whose studies were conducted on Pacific specimens, noted that swordfish began feeding on other fishes at about 21 mm total length. In the larval stage they fed on zooplankton and pelagic fish larvae (as noted by Arata), and in young stages they fed on squids, fishes, and pelagic Crustacea. However, in diet of adults squid were most important, fishes next in importance, and crustaceans seldom taken.

Eschmeyer (1963) reported on the food of two swordfish caught in the Gulf of Mexico. The presence of two species of macrourids, an apogonid, a congrid, a myctophid, and carangids, prompted the author to comment that the presence of near-surface, bathypelagic, and bottom-dwelling fishes in varying stages of digestion in the stomach indicated that the swordfish could withstand a wide range of temperature and pressure while foraging for food.

Manday (1964), in a study of swordfish taken off Cuba during the months of February and March, noted that fishes (a pomfret *Brama brama* and a grouper, the red hind, *Epinephelus guttatus*, plus unidentified fishes) made up 53% of the diet, cephalopods made up about 30%, and crustaceans the remainder.

Tibbo et al. (1961) concluded that substantial numbers of the following species occurred in stomachs: scaled lancetfish (*Paralepis* sp.), lanternfish (*Myctophum* sp.), redfish (*Sebastes marinus*), argentine (*Argentina silus*), silver hake (*Merluccius bilinearis*), squid (*Illex illecebrosus*), stomias (*Stomias boa*), butterfish (*Poronotus triacanthus*), and herring (*Clupea harengus*). These authors included Atlantic salmon (*Salmo salar*) as occurring in swordfish stomachs but there is some doubt of the accuracy of the record.

It is widely accepted that, in general, large predatory fishes eat whatever is available in the greatest numbers in their immediate environment. Food preferences by predators undoubtedly exist but we must assume that the prey species reported here represent both conditions, with greater emphasis on availability. The first six species listed in Table III are fishes known to aggregate in schools and, indeed, many of the other species listed, such as the lanternfishes and the sand lances, are also known to school in large numbers.

It is suggested that when schools of mackerel, barracudinas, herring, or other fishes are encountered during forays for food, a number may be eaten, possibly after being slashed. But individual herring, if encountered, are apparently seldom eaten. This would account for the occurrence of large numbers (up to 30) of herring in a single stomach and the absence of single herring.

A similar argument may be proposed for the mackerel, but here the situation is much more complex since mackerel are used as bait. We suspect also that swordfish may gather bait by cruising along longlines, slashing, and taking bait.

Most studies, including the present one, suggest that the swordfish obtains its food from surface to bottom over a wide depth range, a characteristic it shares with spearfishes such as the white marlin (Wallace and Wallace, 1942), and the striped marlin (Morrow, 1952). It should be noted, however, that studies made prior to 1963 were concerned primarily with female swordfish taken at the surface, and even in the present study no attempt was made to consider sexual differences in food habits.

The importance of mackerel in swordfish diet has been stressed, and it is probably one of the best baits for the longline fishery. It is also apparent that fish is a more important dietary component than squid.

Future studies should include complete identification of ingested organisms, and thus contribute to an understanding of the depths at which feeding occurs. Careful examination of fishes by dissection or, preferably, by X-ray will provide additional information on feeding behaviour. Feeding habits in relation to size and sex of individual swordfish should be considered. And, finally, in order to assess the variations that may occur, samples should be taken both seasonally and throughout the range.

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REFERENCES

ARATA, G. F., JR. 1954. A contribution to the life history of the swordfish, *Xiphias gladius* Linnaeus, from the South Atlantic coast of the United States and the Gulf of Mexico. Bull. Marine Sci. Gulf Caribbean, **4**(3): 183–243.

BECKETT, J. S., AND B. E. BARRETT. 1967. The gempylid *Nealotus tripes*, new to the Canadian Atlantic. J. Fish. Res. Bd. Canada, **24**(5): 1177–1178.

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. U.S. Fish Wildlife Serv., Fish. Bull. No. 53. 577 p.

BRIGGS, J. S. 1958. A list of Florida fishes and their distribution. Bull. Fla. State Museum, Biol. Sci., **2**(8): 223–318.

CLARK, A. H. 1886. Notes on the New England fishery for swordfish during the season of 1884. Rept. U.S. Comm. Fish Fish. 1884, **12**: 233–239.

ESCHMEYER, W. N. 1963. A deepwater trawl capture of two swordfish, *Xiphias gladius*, in the Gulf of Mexico. Copeia, **1963**(3): 590.

GIBBS, R. H. 1960. *Alepisaurus brevirostris*, a new species of lancetfish from the western North Atlantic. Breviora, Museum Comp. Zool., No. 123. 14 p.

GIBBS, R. H., AND N. J. WILIMOVSKY. 1966. Family Alepisauridae. *In* Fishes of the western North Atlantic. Sears Found. Marine Res., Memoir, **1**(5): 482–497.

GOODE, G. B., AND T. GILL. 1887. American fishes. L. C. Page and Co., Boston, Mass., 1887 (1903). 562 p.

GREGORY, W. K., AND G. MILES CONRAD. 1937. The comparative osteology of the swordfish (*Xiphias*) and the sailfish (*Istiophorus*). Am. Museum Novitates, No. 952. 25 p.

GREY, MARION. 1953. Fishes of the family Gempylidae, with records of *Nesiarchus* and *Epinnula* from the western Atlantic and descriptions of two new subspecies of *Epinnula orientalis*. Copeia, **1953**(3): 135–141.

HAEDRICH, R. L. 1964. Food habits and young stages of North Atlantic *Alepisaurus* (Pisces, Iniomi). Breviora, Museum Comp. Zool., No. 201. 15 p.

HAFFNER, RUDOLPHE E. 1952. Zoogeography of the bathypelagic fish, *Chauliodus*. Syst. Zool., **1**: 112–133.

HOUOT, G. 1958. Four years of diving to the bottom of the sea. Natl. Geograph. Mag., **113**(5): 715–731.

KINGSLEY, J. S. 1922. The food habits of swordfish. Science, **56**: 225–226.

LEIM, A. H., AND W. B. SCOTT. 1966. Fishes of the Atlantic coast of Canada. Bull. Fish. Res. Bd. Canada, No. 155. 485 p.

MANDAY, DARIO-GUITART. 1964. Biologia pesquera del Emperador o pez de Espana, *Xiphias gladius* Linneaus (Teleostomi: Xiphiidae) en las aguas de Cuba. Poeyana, Inst. Biol., Acad. Cien Rep. Cuba, Ser. B, **1**: 1–37.

MORROW, J. E. 1952. Food of the striped marlin from New Zealand. Copeia, **1952**(3): 143–145.

PARR, A. E. 1933. Swordfish stomach records. Ibid., **1933**(4): 176–179.

ROFEN, R. R. 1966. Family Paralepididae. *In* Fishes of the western North Atlantic. Sears Found. Marine Res., Memoirs, **1**(5): 205–461.

SCOTT, W. B., AND E. J. CROSSMAN. 1959. The snake-eel *Omochelys cruentifer*, in Canadian Atlantic waters. Copeia, **1959**(4): 344–345.

TIBBO, S. N., L. R. DAY, AND W. F. DOUCET. 1961. The swordfish (*Xiphias gladius* L.) its life history and economic importance in the northwest Atlantic. Bull. Fish. Res. Bd. Canada, No. 130. 47 p.

WALLACE, D. H., AND E. M. WALLACE. 1942. Observations on the feeding habits of the white marlin *Tetrapterus albidus* Poey. Chesapeake Biol. Lab., Bd. Nat. Res., Solomons, Md. Publ. No. 50. p. 3–10.

YABE, H., S. UEYANAGI, S. KIKAWA, AND H. WATANABE. 1959. Study on the life-history of the swordfish, *Xiphias gladius*, Linnaeus. Rept. Nankai Reg. Fish. Lab., No. 10. p. 107–150.

Production of Trimethylamine in Frozen Cod Muscle[1]

By C. H. Castell, D. M. Bishop, and Wanda E. Neal

Fisheries Research Board of Canada
Halifax Laboratory, Halifax, N.S.

ABSTRACT

Trimethylamine (TMA) was produced in frozen cod fillets and in scallop muscle under conditions where bacterial activity could not take place. The amounts formed were smaller than those which usually accompany bacterial deterioration of unfrozen fish. Decreases in storage temperature between −3 and −26 C reduced the rate of TMA formation. At −26 C no measurable increase of TMA was produced in cod fillets during storage periods up to 700 days.

TMA formation appeared to be related to other chemical changes taking place in the frozen muscle. It followed shortly after the formation of free fatty acids and was almost simultaneous with changes taking place in the amounts of extractable protein.

INTRODUCTION

During 1966 and 1967 a series of tests were carried out in this laboratory to follow some of the changes that were taking place in fillets of cod and other fish that had been frozen and stored at several different temperatures. Among other tests, trimethylamine (TMA) determinations were made, principally to test the belief that TMA is not formed in the stored muscle under conditions that prevent bacterial activity. Contrary to our expectations, the TMA did increase in many of the stored frozen fillets. This paper deals with these increases, the conditions under which they occurred, and their probable relationship to other changes that took place in the frozen fish.

It has long been known that trimethylamine oxide (TMAO) in the flesh of many species of marine fish is frequently converted after death into TMA. Early investigators, working mainly with groundfish, found the TMAO in the muscle was not converted into TMA in the absence of bacteria. They also found a close correlation between the numbers of bacteria in the muscle and the amount of TMA that had been formed. As a result of these investigations it was generally accepted that the production of TMA in fish was brought about exclusively by bacterial enzymes. Later it was found that the dark muscle of certain pelagic fish contained enzymes capable of reducing TMAO to TMA (Kawabata, 1953). Jakobsen and Mathieson (1946) and Ronald and Jakobsen (1947) showed that corrosion of cans used for fishery products was accelerated through the interaction of TMAO and the metal of the cans. This also resulted in increased TMA values for the can contents. Vaisey (1956) observed that small concentrations of Fe^{+++} and Fe^{++}, especially in the presence of free cysteine, reduced TMAO to TMA at 22–

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24 C. In this laboratory we have recently found that very small concentrations of bivalent vanadium ions will reduce TMAO to TMA at 0 C. In brief, therefore, the reduction of TMAO to TMA has generally been considered to be the result of bacterial activity, except where it occurs in the dark muscle of some pelagic fish, or where certain metal catalysts are present.

Not much consideration has been given to the formation of TMA in frozen fish. Freezing inhibits bacterial activity and retards the action of most tissue enzymes. It has been generally accepted that TMAO is not reduced to TMA during frozen storage and that the presence of considerable amounts of TMA in frozen fish indicates that bacterial deterioration took place before it was frozen. This viewpoint has been supported by some relatively short-term storage experiments (Good and Stern, 1955; Hartshorne and Puncochar, 1951; Schram, 1953) that were chiefly concerned with fish frozen in vessels at sea before being processed in the plants. Puncochar (1949) observed a limited rise in TMA in frozen fillets up to 3 months and then a decline; and some of the data in the paper of Good and Stern (1955) also suggest increasing TMA content with storage of frozen flounder fillets up to 24 weeks. Pivnick (MS, 1949) working with cod muscle, found no increase in TMA during freezing but an unexplained, small increase during frozen storage. This increase was greater for fish held at −12 than at −23 C.

Banks (1965), discussing "technical problems in the control of deteriorative changes in frozen fish requiring more knowledge from fundamental research," suggests that reactions involving TMAO may well be a factor in the development of off flavours.

PROCEDURES

Preparation and freezing of fillets. — The fillets were cut from deep sea, trawler-caught cod and obtained from a local fish plant. In order to obtain uniformly good quality they were specially selected from the vessel's last day's catch. An attempt was made to use only fish that, at the time of freezing, had a TMA value of 0.5 or less and a FFA value of less than 8% of the total lipids. They were filleted and packaged in the plant in 1-lb waxed cardboard containers and overwrapped at the station in heat-sealed, laminated, plastic pouches. The laminate was composed of nylon bonded to saran-coated polyethylene. The fillets were frozen in the station's plate freezer for 1.5 hr at −40 C and then stored in temperature-controlled, refrigerated boxes at −3.3, −12, and −25 C. Periodically 1-lb packages were removed for analyses. Particular care was taken to blend the fish in preparation for the chemical tests before the flesh was completely defrosted and to carry out the tests as rapidly as possible. This was done to eliminate the possibility of bacterial activity in the defrosted muscle. The bacterial content of the stored, frozen fillets was followed by direct microscopical examination; this was supplemented by plate counts when the microscopical examination indicated that the numbers of bacteria were increasing.

Chemical tests. — The TMA determinations were carried out by the picric acid procedure of Dyer (1945, 1950). Some of the samples were also analyzed for TMA using Beatty and Gibbons' (1937) modification of Conway and Byrnes microdiffusion technique (1933). The term "TMA value" is used to indicate the milligrams of TMA nitrogen per 100 g of fish muscle. The free fatty acid (FFA) content of the muscle was determined on lipids extracted by the method of Bligh and Dyer (1959) and expressed as the percentage of FFA in the extracted lipids. The total extractable protein was used as a measure of protein denaturation, using the procedure of Dyer et al. (1950) and Snow (1950). The oxidation of the fish lipids during storage was followed by means of the thiobarbituric acid test, using the procedure of Tarladgis et al. (1960) with the modifications suggested by Castell et al. (1966a, b).

RESULTS

Temperature was a major factor in determining the rate of the TMA increase in the fish muscle during frozen storage. There was no detectable increase in cod fillets stored up to 700 days at −26 C (−16 F). There was a slow increase for fillets at −12 C (+10 F) and a fairly rapid increase at −3.3 C (+26 F) (Fig. 1 and 2). The range of TMA values was very much lower than

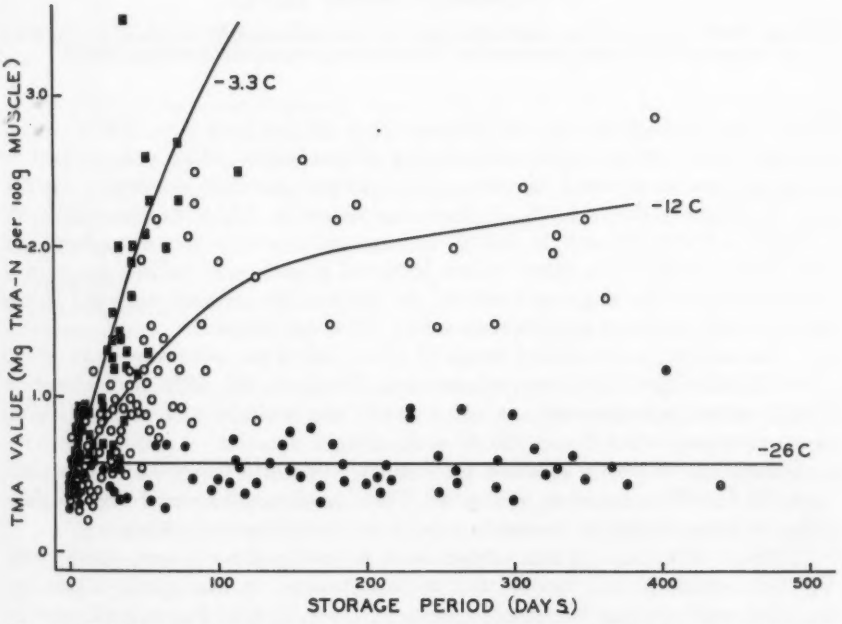

FIG. 1. TMA values of cod fillets, frozen in a plate freezer at −40 C for 1.5 hr and stored at three different temperatures. Values are from eight lots of fish caught at various times throughout the year.

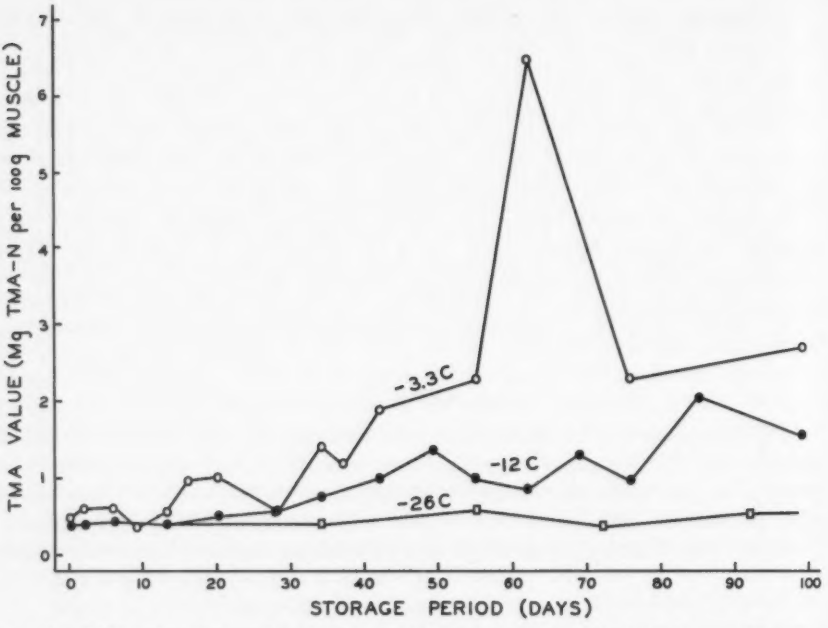

FIG. 2. TMA values for one lot of similar cod fillets from fish caught in February. The fillets were frozen in a plate freezer before being stored at three different temperatures.

those encountered during the deterioration of unfrozen fish. TMA values greater than 5 were rarely encountered. Occasionally, after storage periods ranging between 30 and 80 days, psychrophyllic bacteria developed rapidly on the fillets held at –3.3 C. In these instances the TMA values rapidly increased to levels between 20 and 60, accompanied by very offensive off odours. All TMA values from fillets where bacterial growth was taking place were excluded from the data recorded in the figures. No increase occurred in the number of bacteria on the fillets stored at –10 C and below.

In another, more-limited series of tests, cod fillets were stored at –23 C (–10 F) and –18 C (0 F) for periods up to 200 days. At –23 C no increase in TMA values was observed; at –18 C there was a slight increase, beginning some time between 100 and 150 days of storage.

Two lots of freshly shucked scallops were put into frozen storage at –3.3 and –12 C in March and in November. They developed increased TMA values (Fig. 3) quite similar to those obtained from the frozen cod fillets.

The TMA values given above were determined by Dyer's picric acid method, which is not specific for trimethylamine; it also gives a positive reaction with certain nonvolatile amines (Dyer, 1945). Nonvolatile amines may be present in the more advanced stages of bacterial spoilage, but it is unlikely that they would be produced during any of the changes known to

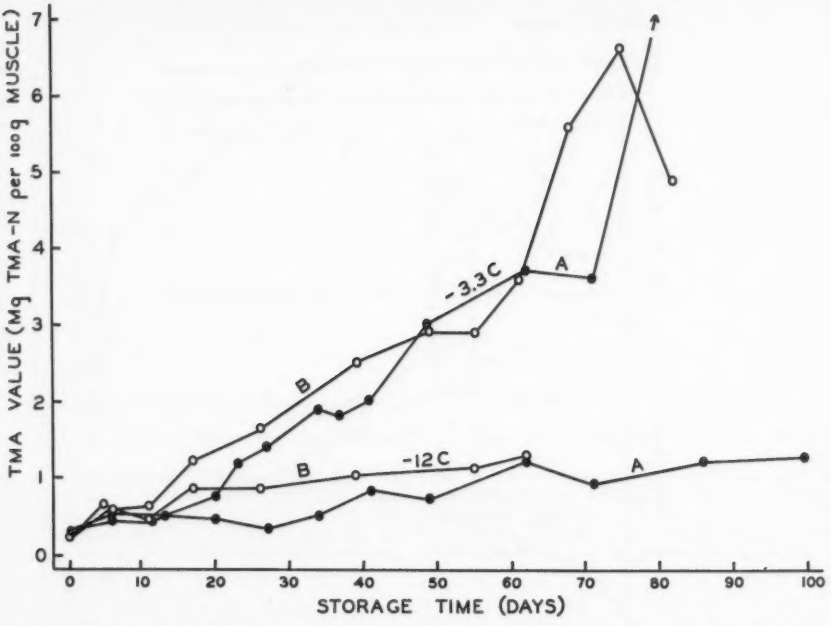

FIG. 3. TMA values of November (A) and May (B) caught scallops in frozen storage. Both lots were frozen for 1.5 hr in a plate freezer before storage at different temperatures.

take place in fish muscle during frozen storage. However, to check this point, parallel TMA determinations were made on frozen stored cod fillets, using Dyer's picric acid method and Beatty and Gibbons' (1937) modification of the microdiffusion technique of Conway and Byrne (1933). The values obtained by the two procedures were very similar, as indicated by the following series of tests:

Fish sample:	A	B	C	D	E
Picric acid test:	0.35	0.97	1.31	2.5	2.7
Conway test:	0.56	0.92	1.60	2.2	2.8

These figures show that the amines present in the muscle were volatile.

Relation between increasing TMA values and other changes taking place in the frozen fillets. — Though simultaneous reactions are not necessarily related, it was of interest to determine whether the increase in TMA values coincided with any of the other chemical changes taking place in the frozen fillets.

In cod fillets stored at −12 C during a period of 200 days there was no change in oxidative rancidity, as indicated by the thiobarbituric acid (TBA) reaction (Fig. 4). Lipid hydrolysis, as indicated by the accumulation of FFA, commenced at the beginning of the storage period. There was no measurable decrease in extractable protein until approximately 20 days had elapsed. It was also about 20 days before the first increase in TMA values began to show up.

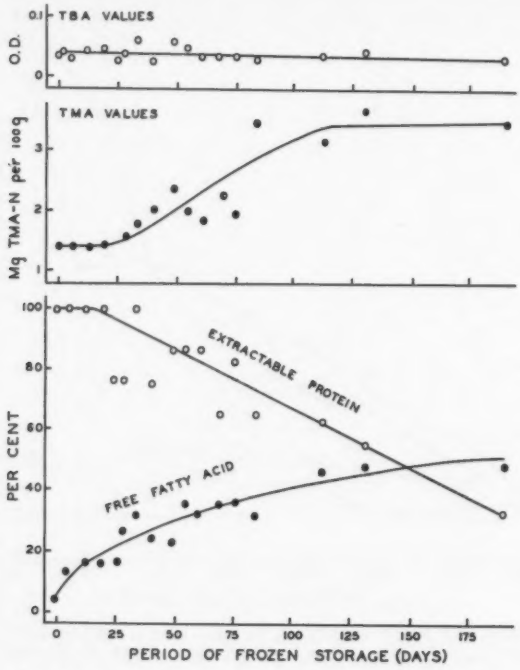

FIG. 4. Some chemical changes occurring during frozen storage of one lot of similar cod fillets. The fillets were frozen in a plate freezer for 1.5 hr and then stored at −12 C (+10 F). Each vertical set of points on the four curves represent values obtained from the same fillets.

These chronological relationships between the development of TMA and changes in the fat and proteins are more evident when TMA values are plotted against the FFA content (Fig. 5) and the percentage decrease in extractable protein (Fig. 6) for each individual sample in the series. In addition to the values obtained for the fillets stored at −12 C, Fig. 5 and 6 include values for samples from the same lot of fish stored at −3.3 C. Irrespective of storage temperature, there appeared to be a straight line relationship between increase in TMA and the decrease in extractable protein. Also, irrespective of the storage temperature, the FFA increased to a level of somewhere between 20 and 30% of the extractable fat before the TMA began to rise. Figures 7 and 8 show similar relationships between TMA and these other changes in a large number of frozen fillets. The values shown represent several lots of fish that were caught, filleted, and put into storage at different periods of the year, and therefore more variable in initial quality than those shown in Fig. 5 and 6. This probably accounts for the greater scatter in the values. However, the same general relationship existed: irrespective of the storage temperature, as the TMA increased, the amount of extractable protein decreased, until

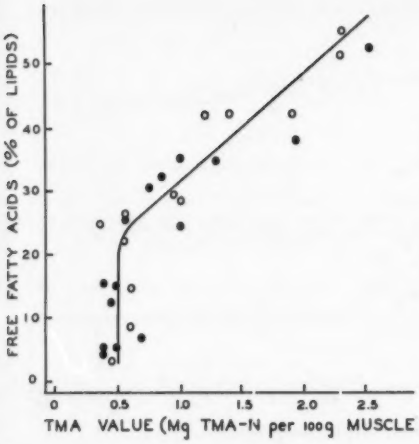

FIG. 5. Relationship between TMA and free fatty acid values for one lot of cod fillets stored for various periods at −12 C (○) or −3.3 C (●). The fillets were initially uniform in quality, and they were frozen in a plate freezer before storing at the different temperatures.

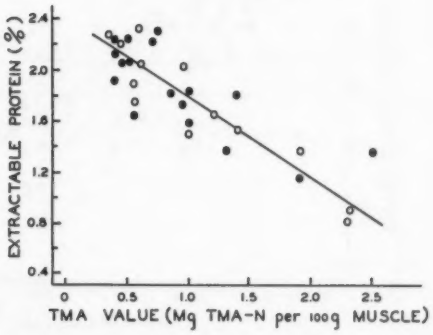

FIG. 6. Relationship between TMA and extractable protein values for one lot of frozen cod fillets stored for various periods at −12 C (○) or −3.3 C (●). These values were obtained from the same lot of fillets shown in Fig. 5.

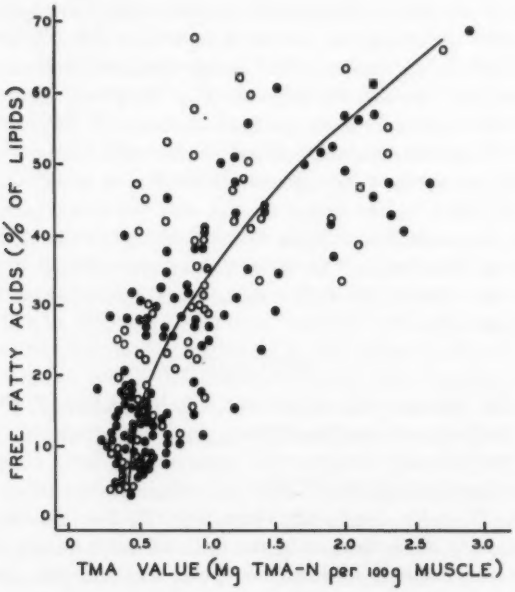

FIG. 7. Relationship between TMA and free fatty acid values for eight lots of frozen cod fillets from fish caught at different times of the year. All fillets were frozen in a plate freezer before storage at −12 C (○) or −3.3 C (●).

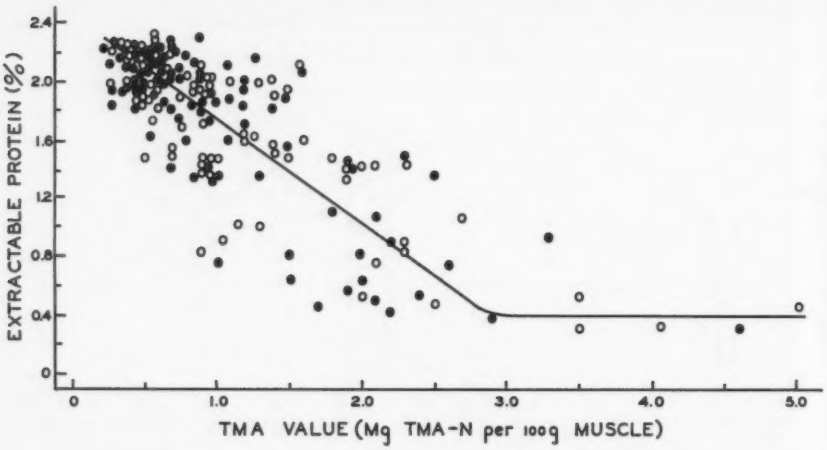

FIG. 8. Relationship between TMA and extractable protein values for eight lots of frozen cod fillets from fish caught at different times of the year. All fillets were frozen in a plate freezer storage at −12 C (○) or −3.3 C (●).

approximately 70% had become inextractable; after this there was no further change. It was also observed, during a very large number of examinations, that TMA never formed in frozen fish muscle under storage conditions that prevented protein denaturation, even though the FFA had increased. For example, cod fillets in storage at −26 C were removed periodically and tested for TMA, FFA, and extractable protein (Fig. 9). From the beginning of the storage period there was a slow, gradual increase in FFA. Up to 700 days there was no measurable change in either extractable protein or TMA values. In tests at higher temperatures, once the FFA had reached values of approximately 20% the TMA values began to rise and the extractable protein began to decrease. In this experiment with the cod fillets at −26 C, the FFA values are now reaching the critical 20–30% values. It will be interesting to see whether either or both of the other values begin to change during the next few months of storage.

DISCUSSION

These results indicate that under certain conditions TMA will form in the muscle of codfish and scallops during frozen storage. There is reason to believe (from preliminary results of experiments now being carried out) that under the same conditions TMA will also be formed in the muscle of frozen haddock, flounder, and other lean fish. So far, no experiments have been carried out with fatty fish, or in the isolated dark muscle of the lean fish.

The TMA was formed in most of these frozen fillets under conditions where bacterial growth was completely inhibited and in muscle that had a very low initial bacterial contamination. Its formation, therefore, was not due to bacterial activity.

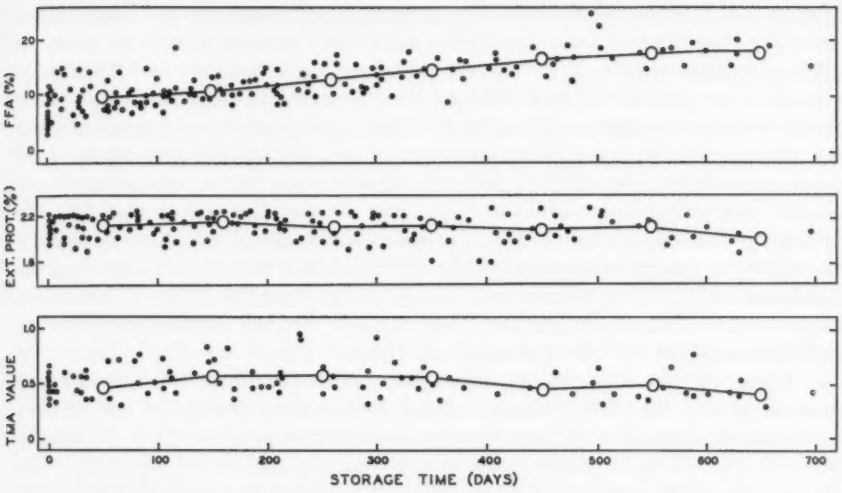

FIG. 9. Free fatty acid, extractable protein, and TMA values for frozen cod fillets stored up to 700 days at −26 C. The large circles connected by lines are the mean values for all tests done during each 100-day interval.

The amounts of TMA formed in frozen fish were much less than the amounts that usually form during bacterial deterioration of unfrozen fish. With fillets having uniformly low initial TMA values (0.3–0.5), during storage these values gradually increased to levels between 2.0 and 3.0, and occasionally to between 3.0 and 7.0. The rate of increase depended upon the storage temperature: the higher the temperature the faster the increase. It was extremely slow at −18 C and there was no evidence of any increase up to 700 days of storage at −26 C.

These results suggest the need for a slight modification in the idea that the TMA values of frozen stored fish are solely the result of bacterial spoilage that took place before the fish were frozen. Certainly very high TMA values (15–50 or more) would indicate poor initial quality before freezing, or that the fish had become defrosted during storage. On the other hand, the TMA values of top quality cod fillets (under 1.0 before freezing) may increase during frozen storage to the TMA values of 1.5–7.0, which are usually associated with second grade fish (Castell and Triggs, 1955; Castell et al., 1958; Castell and Greenough, 1958).

Frequently, government inspectors who are interested in the end-of-the-line quality of fresh fillets will freeze their samples for later TMA determinations. When this procedure is carried out, precautions should be taken to see that the fillets awaiting analysis are not inadvertently stored under conditions that would permit further increase in the TMA values. The best method would be to store the fillets at −23 C (−10 F) or below, until they can be analysed.

It is important to note that the formation of TMA in the frozen fillets occurred only under those conditions that also permitted accumulation of FFA and denaturation of the muscle proteins. The formation of FFA always preceded the production of TMA and the decreases in extractable protein in these stored cod fillets, although J. Olley (personal communication) has assured us that by using other measures of protein denaturation there is no lag between hydrolysis of the lipids and denaturation of the protein in results of the British workers. Irrespective of the temperature of storage, it was found that plotting TMA values against the changes in extractable protein resulted in a straight line relationship. This suggests the almost simultaneous production of TMA and denaturation of protein. Presumably the TMA comes from the TMAO in the muscle, so that one could also say protein denaturation was accompanied by the reduction of TMAO.

These observations prompt some speculation regarding the interrelation of some of the reactions that take place during deterioration of fish muscle in frozen storage. It has been known for some time that FFA formation precedes protein denaturation in frozen fish muscle (Dyer and Morton, 1956; Dyer et al., 1956; Dyer and Fraser, 1959). It has been observed that the fatty species of fish are less subject than lean fish to denaturation during frozen storage (Dyer and Fraser, 1959). Dyer and his associates suggested that the unhydrolyzed, neutral lipids associated with the protein in a manner that protected the molecule against denaturation; also that the liberated fatty acids had the opposite effect and "sensitized" the protein to denaturation (Dyer and Dingle, 1961; Dyer, 1967). Anderson and her associates (Anderson et al., 1963) found that unsaturated FFA added to cod muscle decreased the amount of extractable protein. They also demonstrated that proteins in muscle having a high lipid content showed greater stability than muscle with low fat content towards added FFA (Anderson and Steinberg, 1964), and this was later confirmed by Hanson and Olley (1965).

There is another aspect of the picture that must be taken into consideration: this is the *apparent* absence of oxidation of the highly unsaturated lipids in the cod muscle, and especially the more easily oxidized free fatty acids (Cardin and Bordeleau, 1957; Dyer and Fraser, 1959; Castell and Boyce, 1966). The term "apparent" is purposely emphasized. The fact is that only oxidation as indicated by increased peroxide or TBA values does not occur or has not been observed. It is possible that free radicals produced by peroxidizing fatty acids may react with proteins to form insoluble polymers, resulting in protein denaturation and the removal of these products of lipids oxidation. This type of reaction is not uncommon and there have been many papers recording the damage to enzymes and other proteins by peroxidizing lipids (Andrews et al., 1965; Desai and Tappel, 1963; Roubal, MS, 1965; Roubal and Tappel, 1966a, b; Toyomizu et al., 1963; Wills, 1959, 1960, 1961). Olley and Duncan (1965) have been more specific. They reported that oxidized fatty acids were more effective in aggregating cod muscle myosin than unoxidized acids. They also point out that Ota and Nishimoto (1963) found oxidized fatty

acids more effective than unoxidized acids in solubilizing mackerel muscle proteins. It seems probable, therefore, that one must look to the oxidizing fatty acids, rather than the fatty acids per se, as the instigators of protein denaturation in the frozen muscle. It would explain why FFA formation precedes protein denaturation, and why at times there may be some accumulation of FFA before denaturation of the protein takes place (Dyer, 1967).

The results of this paper suggest that oxygen liberated by the reduction of TMAO may play some part in the oxidation of the fatty acids in the muscle.

In lean fish, the lipids, mostly as phospholipids, are distributed in discrete portions of the cell, and once they have been hydrolyzed, the liberated fatty acids are in immediate contact with the cell proteins (Hanson and Olley, 1965). In the fatty fish, on the other hand, the liberated fatty acids are more likely to remain in solution in the neutral fat. Oxidation of FFA in the lean fish is followed by their reaction with the protein, whereas in the fatty fish the products of oxidation accumulate, resulting in rancidity. If this hypothesis is correct, protein denaturation in cod muscle may actually be a measure of the extent of lipid oxidation that has taken place.

REFERENCES

ANDERSON, M. L., F. J. KING, AND M. A. STEINBERG. 1963. Effect of linolenic, linoleic and oleic acids on measurement of protein extractability from cod skeletal muscle using the solubility test. J. Food Res., **28**: 286–288.

ANDERSON, M. L., AND M. A. STEINBERG. 1964. Effect of lipid content on protein-sodium linolenate interaction in fish muscle. J. Food Sci., **29**: 327–330.

ANDREWS, F., J. BJORKSTEN, F. B. TRENK, A. S. HENIK, AND R. B. KOCH. 1965. The reaction of an autoxidized lipid with proteins. J. Am. Oil Chemists' Soc., **42**: 779–781.

BANKS, A. 1965. Technological problems in the control of deteriorative changes in frozen fish requiring more knowledge from fundamental research. *In* R. Kreuzer [ed.] The technology of fish utilization. Fishing News (Books) Ltd., London. p. 89–91.

BEATTY, S. A., AND N. E. GIBBONS. 1937. The measurement of spoilage in fish. J. Biol. Bd. Canada, **3**: 77–91.

BLIGH, E. G., AND W. J. DYER. 1959. A rapid method of total lipid extraction and purification. Canadian J. Biochem. Physiol., **37**: 911–917.

CARDIN, A., AND M. A. BORDELEAU. 1957. Changes occurring in fat during processing of salt fish. Fish. Res. Bd. Canada, Prog. Rept. Atlantic Coast No. 66. p. 16–20.

CASTELL, C. H., AND G. A. BOYCE. 1966. Erroneous thiobarbituric acid values in fish tissues caused by their normal content of free iron. J. Fish. Res. Bd. Canada, **23**: 1587–1598.

CASTELL, C. H., AND M. E. GREENOUGH. 1958. Grading fish for quality. 3. Grading of recently cut fillets. Ibid., **15**: 729–748.

CASTELL, C. H., M. E. GREENOUGH, R. S. RODGERS, AND A. S. MACFARLANE. 1958. Grading fish for quality: I. Trimethylamine values of fillets cut from graded fish. Ibid., **15**: 701–716.

CASTELL, C. H., B. A. MOORE, AND W. E. NEAL. 1966a. Cause and control of spurious thiobarbituric acid values from fish muscle in the presence of inorganic iron salts. Ibid., **23**: 737–746.

CASTELL, C. H., B. A. MOORE, P. M. JANGAARD, AND W. E. NEAL. 1966b. Oxidative rancidity in frozen stored cod fillets. Ibid., **23**: 1385–1401.

CASTELL, C. H., AND R. E. TRIGGS. 1955. Spoilage of haddock in trawlers at sea; measurement of spoilage and standards of quality. J. Fish. Res. Bd. Canada, **12**: 329–341.

CONWAY, E. J., AND A. BYRNE. 1933. An absorption apparatus for the micro-determination of certain volatile substances. I. The micro-determination of ammonia. Biochem. J., **27**: 419–429.

DESAI, I. D., AND A. L. TAPPEL. 1963. Damage to proteins by peroxidized lipids. Lipid Res., **4**: 204–207.

DYER, W. J. 1945. Amines in fish muscle. I. Colorimetric determination of trimethylamine as the picrate salt. J. Fish Res. Bd. Canada, **6**: 351–358.
1950. Note on the colorimetric estimation of trimethylamine. Ibid., **7**: 576–579.
1967. Frozen fish muscle — chemical changes and organoleptic quality. Cryobiology, **3**: 297–305.

DYER, W. J., AND J. R. DINGLE. 1961. Fish proteins with special reference to freezing. *In* G. Borgstrom [ed.] Fish as food. Academic Press, Inc., New York. Chap. 9.

DYER, W. J., AND D. I. FRASER. 1959. Proteins in frozen fish. 13. Lipid hydrolyses. J. Fish. Res. Bd. Canada, **16**: 43–52.

DYER, W. J., H. V. FRENCH, AND J. M. SNOW. 1950. Proteins in fish muscle. I. Extraction of protein fractions in fresh fish. Ibid., **7**: 585–593.

DYER, W. J., AND M. L. MORTON. 1956. Storage of frozen plaice fillets. Ibid., **13**: 129–134.

GOOD, C. M., AND J. A. STERN. 1955. Effect of iced and frozen storage upon the trimethylamine content of flounders (*Parophyrs vetulus*). Food Technol., **9**: 327–331.

HANSON, S. W. F., AND JUNE OLLEY. 1965. Observations on the relationship between lipids and protein denaturation. *In* R. Kreuzer [ed.] Technology of fish utilization. Fishing News (Books) Ltd., London. p. 111–115.

HARTSHORNE, J. C., AND J. F. PUNCOCHAR. 1951. Studies of roundfish frozen at sea, New England species. Food Technol., **5**: 492–495.

JAKOBSEN, F., AND E. MATHIESON. 1946. Corrosion of containers for canned foods. Skrifter Norske Videnskaps, Oslo. I. Mat. Naturv. Klasse, **5**: 6–112.

KAWABATA, T. 1953. Studies on trimethylamine oxide reductase. I. Reduction of trimethylamine oxide in dark muscle of pelagic migrating fish under aseptic conditions. Bull. Japan. Soc. Fish., **19**: 505–512.

OLLEY, J., AND R. H. DUNCAN. 1965. Lipids and protein denaturation in fish muscle. J. Sci. Food Agr., **16**: 99–104.

OTA, F., AND J. I. NISHIMOTO. 1963. On the effects of lipids and related substances on denaturation of protein in frozen fish muscle through storage. Bull. Inst. Intern. Froid. p. 874 (abstr.).

PIVNICK, H. MS, 1949. Bacteriological and biochemical studies of the rate of decomposition of unfrozen and defrosted cod muscle. M.Sc. Thesis. Dalhousie University, Halifax, Nova Scotia.

PUNCOCHAR, J. F. 1949. Freezing roundfish aboard boats. Atlantic Fisherman, **30**: 17 and 26.

RONALD, A. O., AND F. JAKOBSEN. 1947. Trimethylamine oxide in marine products. J. Soc. Chem. Indust., **66**: 160–166.

ROUBAL, W. T. MS, 1965. Lipid peroxidation damage to biological materials. Ph.D. Thesis. Univ. of California, Davis, California. University Microfilms, Inc., Ann Arbor, Michigan.

ROUBAL, W. T., AND A. L. TAPPEL. 1966a. Damage to proteins, enzymes and amino acids by peroxidizing lipids. Arch. Biochem. Biophys., **113**: 150–155.
1966b. Polymerization of proteins induced by free-radical lipid peroxidation. Ibid., **113**: 15–155.

SCHRAM, E. 1953. Chemical determination of volatile odorant substances coming from fish in the course of their preservation at low temperatures. Inst. Intern. Froid, J. Mons, Belg. Communs., 229–233.

SNOW, J. M. 1950. Proteins in fish muscle. II. Colorimetric estimation of fish muscle protein. J. Fish. Res. Bd. Canada, **7**: 594–598.

TARLADGIS, B. G., BETTY M. WATTS, M. T. YOUNATHAN, AND L. DUGAN, JR. 1960. A distillation method for the quantitative determination of melonaldehyde in rancid foods. J. Am. Oil Chemists' Soc., **37**: 44–48.

TOYOMIZU, M., Y. MATSUMURA, AND Y. TOMIYASU. 1963. Lipid oxidation and protein denaturation in freeze-dehydrated fish. Bull. Japan. Soc. Sci. Fish., **29**: 854–859.

VAISEY, E. B. 1956. The non-enzymic reduction of trimethylamine oxide to trimethylamine, dimethylamine and formaldehyde. Canadian J. Biochem. Physiol., **34**: 1085–1090.

WILLS, E. D. 1959. Effect of some organic peroxides on sulphydryl enzymes. Biochem. Pharmacol., **2**: 276–285.

1960. Enzyme inhibition by oxidized unsaturated fatty acids. Proc. Intern. Conf. Biochem. Lipids, Marseilles.

1961. Effect of some unsaturated fatty acids and their peroxides on enzymes. Biochem. Pharmacol., **7**: 7–16.

Changes in Free Amino Acids in Skeletal Muscle of Cod (*Gadus morhua*) Under Conditions Simulating Gillnet Fishing[1]

By N. Dambergs and P. Odense

Fisheries Research Board of Canada
Halifax Laboratory, Halifax, N.S.

AND

R. Guilbault

Fisheries Research Board of Canada
Technological Station, Grande-Rivière, P.Q.

ABSTRACT

The total amounts of free amino acids, comprising both the intracellular and plasmal pools, as well as the amino acids combined in small peptides were determined with an automatic amino acid analyser in muscular tissues of freshly killed cod and in cod suffocated in simulated gillnetting conditions. The total amount of the free amino acids in the musculature was 2.4% of the amino acids composing the proteins. More than 90% of the free amino acid pool was represented by histidine, taurine, glycine, alanine, lysine, and β-alanine. The amino acids that were not found in small peptides are taurine, alanine, threonine, lysine, tyrosine, cystine, and methionine. In the absence of flexion or handling of the suffocated fish there was no evidence of enzymatic processes up to 72 hr after death. There was a slight, continuous loss of the free amino acids from the intact body of the fish during the prerigor and rigor periods. No evidence of deaminase activity affecting the amino acids was detected. Histidine, with its methyl homologues, was the major free amino acid.

INTRODUCTION

Fillets prepared from cod caught in gillnets are frequently inferior in quality to those obtained from cod caught by other conventional fishing methods. Such fillets are apt to undergo rapid autolysis and often the flesh of the gillnetted cod disintegrates before reaching the filleting line. The mechanism which promotes this rapid deterioration is not fully understood, and to gain some insight into this problem experiments were performed in which cod were subjected to simulated gillnetting conditions. Attention was focused on the postmortem changes in the initial levels of free amino acids (FAA) in the cod musculature.

Surveys of the literature reported by Simidu (1961) and by Geiger and Borgstrom (1962) reveal that there is an abundant literature describing various aspects of FAA in fish, but there is an almost total lack of complete FAA analyses of fish muscle. Florkin (1956) explored the role of FAA in some

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terrestrial and aquatic animals. More recently Konosu et al. (1964) have described the FAA content of red sea bream, striped mullet, and eel.

The purpose of this study was first to determine the composition of the FAA pool in muscle of freshly killed North Atlantic cod and then explore the changes in the FAA pool in strangulated cod during a period of 72 hr after the gills were immobilized. This period is equivalent to that between death and the beginning of the industrial processing.

MATERIALS AND METHODS

Cod caught in November in the Bay of Chaleur were kept in recirculating seawater tanks at 4 C until the following March and April when required. The fish fed regularly and postmortem inspection of the inner organs did not reveal any pathological changes. The occurrence of empty stomachs (25%) was nearly the same as that generally observed with freshly trawled cod (20%).

A total of 16 fish (Table I) were used in four tests using 4 fish each time.

TABLE I. Size and sex of cod used for the various periods after the gills were immobilized.

Hours after gills immobilized	Length (*cm*)		Weight (*g*)		Sex	
	Range	Avg	Range	Avg	Male	Female
0	61–73	67.3	1590–2640	2140	4	–
24	45–67	55.8	940–2070	1480	–	4
48	58–61	59.5	1390–2495	1780	2	2
72	53–76	63.3	1160–3320	2290	1	3

The first test served to establish the concentrations of the FAA and acids combined in small peptides present in muscular tissue of a freshly killed cod. To avoid having the fish struggle, they were taken out of the tank and instantaneously killed. They were immediately filleted, then skinned, and a 100 g sample was taken from the dorso-lateral part of the fillet. The sample was homogenized in a Waring Blendor with 200 ml water for 2+2+1 min with 1-min intervals for cleaning of the baffle and manual stirring. The resulting slurry was centrifuged at 13,000 rpm for 20 min, and the supernates decanted into a viscose dialysing bag. A pressure of 10 lb nitrogen was applied to the homogenate in the bags, and the filtrate was collected overnight at 2 C. A sample was placed in an ampoule, frozen, sealed, and kept frozen until analysed for FAA. Another sample was hydrolysed with twice its volume of HCl 6 N in a sealed, degassed tube for 24 hr at 105 C. After elimination of HCl, the solid residue was re-dissolved in an acetate buffer of *p*H 2.20. The hydrolysates also were kept in sealed ampoules under refrigeration.

In the further three tests the cod were placed in simulated gillnet fishing conditions. An elastic rubber band was fitted around the gills of the cod and

the fish was returned to the aquarium. There the cod swam quietly for periods of 5–20 min, then settled on the bottom, where some died within 30 min and all within 2 hr. Twenty-four hours after the immobilization of gills a first group of four fish was taken out, followed by a second group after 48 hr, and the last after 72 hr. The simulated gillnet fishing conditions were intentionally simplified. There was no wave motion to flex the muscles of the fish. Both the salinity and the temperature were close to the natural conditions prevailing at the time in the open inshore waters. After 72 hr the fish were still in rigor. Amlacher (1961) who surveyed the knowledge concerning the rigor mortis of fish, gives 32–92 hr as the limits for the duration of stiffness for suffocated fishes which are not kept in ice. It may be assumed that after 72 hr the period of rigor was approaching its end. The suffocated fish were processed in the same way as the instantaneously killed fish.

Despite the fact that the extracts were kept frozen, slight turbidity in some ampoules was noticed on re-thawing. To avoid an eventual contamination of the exchange resins, the unhydrolysed samples were treated with sulfosalicylic acid by adding the crystalline reagent to the extract to have 5% final concentration. Zachman et al. (1966) showed that sulfosalicylic acid is superior to perchloric and picric acids as a reagent for deproteinisation. After addition of the reagent, the extracts were syringe-filtered through a Millipore .22 micron filter. The hydrolysates also were filtered but without addition of the sulfosalicylic acid.

The amino acids were determined with an automatic amino acid analyser, an updated Beckman model 120A. The resins used were types AA15 and AA27. Citrate buffers of *p*H 3.28, 4.25, and 5.26 were used for elution at 55.5 C. Beckman's amino acid mixture was used as a standard with eventual addition of taurine, β-alanine, 1-methyl- and 3-methyl-histidine.

RESULTS AND DISCUSSION

Previous investigators have attempted to link the FAA content of fish muscle with its organoleptic quality. Dyer and Dyer (1947) measured the losses of FAA and water-soluble proteins from gutted and iced cod during the transportation of trawl-caught fish to the shore plants. They found 28% of the total FAA was lost during the first 6 days and the losses amounted to 60% after 15 days. In the same period 3.8% of the water-soluble proteins was also leached by the melting ice. The authors concluded that these losses were detrimental to the marketing qualities of the final products.

In a search for an objective standard for the freshness of sea food, Shewan et al. (1952) and Shewan (1953, 1957) studied the nonprotein extractives from various North Sea fish. Jones (1954a, b, 1955a, b) and Hodgkiss and Jones (1955), using the methods described by Shewan (1953), determined the nature of the postmortem changes in the FAA of iced cod, and observed seasonal variations in the levels of some of the amino acids. Hodgkiss and Jones (1955) noted a postmortem uptake of FAA by sterile cod muscle.

Ranke (1960), working with ling and coalfish, also observed a rapid loss of FAA during the first days of storage, but attributed this to bacterial destruction of the amino acids on the surface of the fillet. She confirmed previous findings that β-alanine usually is present in small amounts in very fresh muscle, but increases rapidly in iced storage, which led her to suggest that it be used as an index of freshness.

Bramstedt (1962) studied the relationship between the FAA, carbohydrates and nucleotides, and the market qualities of fisheries products. He emphasized the seasonal variation of the FAA as well as the variations of sugars and nucleotides resulting from the physical exertion suffered by the fish prior to its death.

The first investigation of the enzymes involved in the metabolism of amino acids in cod muscle were made by Siebert et al. (1965). They found that peptidases formed the major group of enzymes, having 10–100 times the activity of the cathepsins, transaminases, and amidases. They concluded that sterile fish muscle can easily degrade proteins to amino acids, but the decomposition of the FAA, leading to the production of undesirable odour and taste substances, is only to be expected in the case of bacterial spoilage.

Nineteen free amino acids in measurable amounts along with ammonia were detected in the muscle (Tables II, III). Tryptophan and hydroxyproline also appeared in a few extracts, but only as traces. The methods used did not register such compounds as trimethylamine oxide, creatine, betaine, and purines, known to be present in aqueous cod muscle extracts. Histidine, 1-methyl-histidine, and 3-methyl-histidine emerged as a single peak. Attempts to differentiate the histidines by thin-layer chromatography gave inconclusive results. No 3-methyl-histidine could be detected in the extracts and histidine and 1-methyl-histidine appeared to be present in approximately equal amounts. Jones (1954b) reported 1-methyl-histidine to be present in moderate amounts and histidine only in trace amounts in *Gadus callarias*, whereas our findings show that in North Atlantic cod the sum of the histidines is the major component of the FAA pool. More than 90% of the FAA pool was represented by histidines, taurine, glycine, alanine, lysine, and β-alanine. The FAA pool constituted only 2.4% of the amino acids composing the proteins.

Of the 19 amino acids, all but 6 showed an increase after hydrolysis of the extracts. The amino acids not involved in peptides are taurine, alanine, lysine, cystine, methionine, and tyrosine.

Taurine, glycine, alanine, lysine, serine, glutamic acid, and cystine generally decreased with time after death (Table II). The concentrations of only phenylalanine and arginine increased with time. Tyrosine concentrations remained practically constant. The variations of threonine and methionine were inconclusive because of the instability of these compounds. Valine, proline, leucine, isoleucine, aspartic acid, histidine, and β-alanine increased only towards the end of the 72-hr period. It is noteworthy that on hydrolysis of the extracts the molar increase of histidine in the first three

TABLE II. Concentrations of water extractable amino acids and ammonia (micromoles per 100 g of muscle) in cod muscle before hydrolysis of the extract. Averages are for four fish.

	Hours after gills immobilized							
	0		24		48		72	
	Range	Avg	Range	Avg	Range	Avg	Range	Avg
1. Taurine	526–876	686	498–855	666	416–574	505	391–508	438
2. Histidine	454–812	571	236–462	372	112–566	351	400–896	640
3. Glycine	378–773	528	245–399	323	505–606	560	64–637	396
4. Alanine	323–535	413	206–384	274	113–386	224	150–476	293
5. β-Alanine	211–413	287	197–248	220	161–300	232	186–430	307
6. Lysine	161–251	213	151–304	216	92–223	172	57–122	94
7. Serine	57–116	87	39–92	66	17–56	38	17–60	48
8. Glutamic acid	62–88	73	36–60	43	27–80	43	41–73	63
9. Threonine	36–49	43	31–130	62	28–55	35	24–55	39
10. 1/2 Cystine	28–53	41	18–46	36	0–35	11	0–24	18
11. Valine	18–35	28	20–31	24	15–59	29	24–52	34
12. Proline	20–36	25	10–42	28	10–41	24	13–69	31
13. Leucine	15–29	24	21–27	24	14–63	29	18–60	34
14. Methionine	18–32	24	56–70	66	20–42	29	14–27	21
15. Aspartic acid	15–27	20	20–27	21	21–27	24	21–36	25
16. Tyrosine	11–21	15	8–17	13	8–29	17	10–24	15
17. Isoleucine	8–18	14	10–13	11	7–39	18	11–38	20
18. Phenylalanine	7–13	8	8–17	13	11–39	18	8–32	17
19. Arginine	4–14	8	4–22	13	6–17	11	7–15	11
Total	2352–4191	3108	1814–3246	2491	1583–3237	2370	1456–3634	2544
Ammonia	778–830	813	1009–1242	1121	918–1182	1064	881–1189	1011

sets of experiments was about double that of the β-alanine. In the last set (72 hr) the increases were about equal. This indicates that not all of the combined amount of histidines was derived from anserine. There must be other histidine-containing peptides in cod muscle besides the β-alanyl-1-methyl-histidine.

The variations of the concentrations of the amino acids from fish to fish in both hydrolysed and nonhydrolysed extracts were considerable. Cystine, which was absent in two original and one hydrolysed extract, and glycine showed the greatest variations.

During the 72-hr postmortem period, the bodies of the fish remained intact and immobile. The bacterial activity in muscle tissues in such conditions is negligible. It was anticipated that any activity of the endogenous proteolytic enzymes would be reflected by increases in the concentrations of both the FAA and peptides. The overall changes in FAA before hydrolysis (Table IV) indicate that at 48 hr after death the total FAA was 26% below the initial value; at 72 hr the concentration increased somewhat. The decrease in FAA appears to be accounted for by an uptake of the amino acids

TABLE III. Concentrations of water extractable amino acids and ammonia (micromoles per 100 g of muscle) in cod muscle after hydrolysis of the extract. Averages are for four fish.

	Hours after gills immobilized							
	0		24		48		72	
	Range	Avg	Range	Avg	Range	Avg	Range	Avg
1. Taurine	445–809	644	546–846	697	448–609	521	389–519	440
2. Histidine	685–1334	834	549–1182	728	587–830	701	582–935	721
3. Glycine	886–1247	998	757–906	857	937–1149	1065	461–1099	881
4. Alanine	276–522	400	230–417	294	133–430	323	164–512	308
5. β-Alanine	245–683	413	297–626	414	368–508	421	322–522	402
6. Lysine	144–181	167	130–248	206	151–185	168	158–169	164
7. Serine	76–126	99	60–111	87	38–81	63	31–81	67
8. Glutamic acid	78–122	102	63–91	74	50–137	88	56–104	88
9. Threonine	42–48	45	39–115	64	35–71	48	28–64	45
10. 1/2 Cystine	17–42	29	27–59	41	7–31	15	0–21	14
11. Valine	17–49	35	28–34	31	28–76	46	28–62	39
12. Proline	35–52	42	20–49	41	34–76	48	42–66	55
13. Leucine	17–52	39	31–35	34	24–85	50	28–71	41
14. Methionine	18–32	25	13–24	18	14–38	21	11–27	21
15. Aspartic acid	13–48	38	27–38	31	24–55	42	29–42	34
16. Tyrosine	8–13	11	11–28	17	7–25	15	11–17	14
17. Isoleucine	10–27	20	17–21	20	14–48	28	14–34	24
18. Phenylalanine	10–34	28	20–32	28	21–55	36	22–42	31
19. Arginine	10–17	13	11–24	15	14–38	22	10–88	34
Total	5234–7875	3982	2876–4886	3697	2934–4527	3721	2386–4475	3423
Ammonia	2202–2437	2330	2026–2521	2289	2362–2647	2509	1809–2419	2152

TABLE IV. Concentrations of amino acids and ammonia (milligrams per 100 g muscle) before and after hydrolysis of extracts, and increases in peptide fraction.

Hours after gills immobilized	Amino acids			Ammonia	
	Before	After	Increase in peptide	Before	After
0	365	454	89	14	40
24	299	423	124	19	39
48	271	416	145	18	43
72	303	389	86	17	37

into the peptide fraction, which increased up to 48 hr postmortem and decreased at 72 hr postmortem. This explanation is in agreement with the finding that the concentrations of ammonia remained practically constant throughout the postmortem period. There was no indication of any deaminase activity in the musculature of an expired, but intact and immobile, cod during

the prerigor and rigor periods. The increase of ammonia after hydrolysis of the extracts can be ascribed largely to the degradation of nucleotides and to a much lesser extent to the hydrolytic deamination of the hydroxylated amino acids or asparagine and glutamine.

These results indicate that there are no drastic changes in the FAA levels in cod muscle up to 72 hr postmortem under the described conditions. There appears to be an initial incorporation of amino acids into peptides followed by a reversal of the trend near the end of the rigor period. The variation in FAA from fish to fish is considerable and indicates the need for sampling as many individuals as possible. The results are in accord with parallel studies on acid phosphatase and cathepsin activity in gillnetted cod (Odense et al., 1968) and indicate that under optimum fishing conditions, gillnetted cod caught in cold water and quickly suffocated will yield first quality fillets even after 2 days in the nets. However, detrimental conditions such as high water temperature, wave motion, and struggling may quickly reduce the quality of the gillnetted cod.

REFERENCES

AMLACHER, E. 1961. Rigor mortis in fish. *In* G. Borgstrom [ed.] Fish as food. Vol. I. Academic Press, Inc., New York, London. p. 385–409.

BRAMSTEDT, F. 1962. Significance of the variations in the contents of nucleotides, free amino acids and carbohydrates of the fish muscle in assessing the quality. Fette Seifen Anstrichmittel, **64**(9): 820–825.

DYER, W. J., AND F. E. DYER. 1947. Losses through the leaching by water from melting ice of soluble constituents in iced, gutted cod. Fish. Res. Bd. Canada, Prog. Rept. Atl. Coast Stations, No. 40. p. 3–5.

FLORKIN, M. 1956. Vergleichende Betrachtungen des stationaeren Zustandes der nicht-eiweiss-gebundenen Aminosäure der Tiere. Vergleichende Biochemische Fragen. Springer Verlag. Berlin. 99 p.

GEIGER, E., AND G. BORGSTROM. 1962. Fish protein-nutritive aspects. *In* G. Borgstrom [ed.] Fish as food. Vol. II. Academic Press, Inc., New York, London. p. 28–114.

HODGKISS, W., AND N. R. JONES. 1955. The free amino acids of fish. Post-mortem changes in sterile skeletal muscle of North Sea codling (*Gadus callarias*). Biochem. J., **61**: iv–v.

JONES, N. R. 1954a. Taurine in fish and iced skeletal muscle of codling (*Gadus callarias*). Ibid., **56**: xxii.

1954b. Factors affecting the free amino acid composition of fresh and iced skeletal muscle of North Sea codling (*Gadus callarias*). Ibid., **58**: vii, xlvii–xlviii.

1955a. The free amino acids of fish. 1-Methyl-histidine and β-alanine liberation by skeletal muscle anserinase of codling (*Gadus callarias*). Ibid., **60**: 81–87.

1955b. The free amino acids of fish. I. Taurine in the skeletal muscle of codling (*Gadus callarias*). J. Sci. Food Agr., **6**: 3–9.

KONOZU, S., M. OZAY, AND Y. HASHIMOTO. 1964. Free amino acids in the muscle of a few species of fish. Bull. Japan. Soc. Sci. Fish., **30**(11): 930–934.

ODENSE, P. H., H. P. DUSSAULT, AND B. WOJTOWICZ. 1968. Effect of simulated gillnetting on some enzymic and organoleptic changes in cod. J. Fish. Res. Bd. Canada. (In press.)

RANKE, E. 1960. Der Einfluss der Lagerung auf die freien Aminosäuren und Peptide beim Lengfisch (*Molva vulgaris*) und Seelachs (*Gadus virens*). Arch. Fischereiwiss., **11**: 18–47.

SHEWAN, J. M. 1953. The nitrogenous extractives from fresh fish muscle. II. Comparison of several gadoid and elasmobranch species. J. Sci. Food Agr., **4**: 565–568.

SHEWAN, J. M., L. I. FLETCHER, S. M. PARTRIDGE, AND R. C. BRIMLEY. 1952. Nitrogenous extractives from fresh haddock muscle: Fractionation with ion-exchange resins. Ibid., **3**: 394–398.

SHEWAN, J. M., AND N. R. JONES. 1957. Chemical changes occurring in cod muscle during chill storage and their possible use as objective indices of quality. Ibid., **8**: 491–498.

SIEBERT, G., A. SCHMITT, AND J. BOTTKE. 1965. Enzymes of the amino acid metabolism in cod muscle. Arch. Fischereiwiss., **15**(3): 233–244.

SIMIDU, W. 1961. Nonprotein nitrogenous compounds. *In* G. Borgstrom [ed.] Fish as food. Vol. I. Academic Press, New York, London. p. 353–384.

ZACHMANN, M., W. W. CLEVELAND, D. G. SANDBERG, AND W. L. NYHAN. 1966. Concentrations of amino acids in plasma and muscle. Am. J. Diseases Children, **112**: 283–289.

Amphipoda of the Atlantic and Arctic Coasts of North America: *Anonyx* (Lysianassidae)[1,2]

By Donald H. Steele

Department of Biology
Memorial University of Newfoundland, St. John's, Nfld.

and

Pierre Brunel[3]

Station de Biologie marine
Grande-Rivière (Gaspé), Québec

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[1]Received for publication October 23, 1967.
[2]Travaux sur les Pêcheries du Québec, No. 22, Direction des Pêcheries, Ministère de l'Industrie et du Commerce, Province de Québec.
[3]Present address: Marine Sciences Centre, McGill University, Montreal 2, Québec.

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ABSTRACT

In place of the widely ranging, abundant, and variable species *Anonyx nugax*, previously recorded from Canadian Atlantic and Arctic waters, eight less variable species of this genus are here recognized, one of which (*sarsi*) is new to science. Detailed descriptions, figures, distribution maps and a key applying to all sizes are given. The study of the species is based on examination of available type-specimens and the use of new characters. The systematics of the genus is discussed in a chronological review of all the relevant literature, and the status of several species is revised.

Since the young of large and small species are similar among themselves, and have sometimes been wrongly described as distinct species, they are also described and illustrated at two sizes. Mature males are distinguished by elongated second antennae equipped with calceoli, in most species by the armature of the second and third uropods, and sometimes by their enlarged eyes.

Three species are characterized by a row of spines accompanying single setae on the hind margin of segment 6 of peraeopods 3–4, and by a rather unprominent upper lip. One may distinguish them as follows. The large (>33 mm) *A. laticoxae* has short spines on peraeopods 3–4, an anteriorly well-expanded first coxa, and an unconstricted short-spined inner ramus of uropod 2. *Anonyx compactus* is smaller (12–17 mm), has one elongated ventral spine on each of the first two flagellar segments of antenna 1, a posterior projection marked off by an angle from the lateral plate of metasome segment 3, a strongly parachelate peraeopod 1 with a perpendicular palm, and a fairly strongly subchelate peraeopod 2. *Anonyx sarsi* is of medium size (20–31 mm), has a very low and unprominent upper lip and, on the outer ramus of uropod 2, small similar-sized spines on the proximal two-thirds of the inner margin (no such spines in *laticoxae* and *compactus*); the female has tufts instead of a row of setae on the dorsal margin of the fourth peduncular segment of antenna 2, but otherwise the species is morphologically similar to *A. nugax*.

The other five species are characterized by a row of pairs of long setae on the hind margin of segment 6 of peraeopods 3–4 and, except *nugax*, have a rather prominent upper lip. Except in *ochoticus* and *lilljeborgi*, uropod 2 bears spines on the inner margin of its outer ramus. *Anonyx ochoticus* is the smallest (9–11 mm) species, and has on urosome segment 1 a prominent dorsal keel well overlapping the next urosome segments. *Anonyx debruyni*, rather small (15–21 mm), has a parachelate peraeopod 1 with an oblique palm, a very strongly subchelate peraeopod 2, most prominent and pointed upper lip and interantennal angle, and, on the outer ramus of uropod 2, only two small spines on the distal half of the inner margin. *Anonyx lilljeborgi* is small (9–18 mm), has a very prominent but high and usually evenly rounded upper lip, a concave cephalic ventral margin (like *debruyni*), and a lateral plate of metasome segment 2 with a nearly toothless postero-ventral corner. *Anonyx nugax* is the largest (31–44 mm) species, with a little-projecting upper lip, a prominent tooth at the postero-ventral corner of metasome lateral plate 2, a short posterior projection, with a nearly straight ventral margin, on the lateral plate of metasome segment 3 and, on the inner margin of the outer ramus of uropod 2, a row of similar-size small spines not extending into the distal third of the ramus. *Anonyx pacificus* is also large (27–34 mm) and similar to *nugax*, but differs in the more prominent and pointed upper lip, the longer and ventrally concave posterior projection on metasome lateral plate 3, and, on the outer ramus of uropod 2, spines which increase in size distally and reach into the distal third of the inner margin.

Three species, *nugax*, *lilljeborgi*, and *sarsi*, have a circumpolar arctic-boreal distribution, the latter chiefly in shallow water (<50 m). Four (*pacificus*, *laticoxae*, *ochoticus*, and *compactus*) are colder-water forms apparently of Pacific origin and all new for the North Atlantic. The distribution of *debruyni* is uncertain.

RÉSUMÉ

Dans l'aire à l'étude nous reconnaissons huit espèces, dont une (*sarsi*) nouvelle pour la science, au lieu de l'espèce (*nugax*) unique, abondante et variable qu'on y avait fréquemment signalée auparavant. Pour ces huit espèces, nous donnons des descriptions et figures détaillées,

des cartes de distribution et une clef applicable aux individus de toutes tailles. Les conclusions sur la nomenclature et l'identité des espèces s'appuient sur l'examen des spécimens-types disponibles et l'utilisation de nouveaux caractères. Une revue chronologique de toute la documentation pertinente encadre une discussion de la systématique du genre et la révision du statut de plusieurs espèces.

Descriptions et illustrations sont fournies des jeunes de deux tailles différentes, puisque les jeunes des grandes et des petites espèces, parfois décrits erronément comme espèces distinctes dans le passé, se ressemblent entre eux. On distingue les mâles adultes par l'allongement et les calcéoles de leurs secondes antennes, par l'armature des seconds et troisièmes uropodes, et parfois par l'expansion des yeux.

Trois espèces se distinguent par la rangée d'épines appariées chacune à une soie au bord postérieur du 6e segment des 3e et 4e péréiopodes, et par un labre assez peu proéminent. L'accent étant mis sur les caractères exclusifs des adultes et la taille à maturité, on peut séparer les espèces comme suit. *Anonyx laticoxae*, de grande taille (>33 mm), porte des épines trapues sur les 3e et 4e péréiopodes, une première plaque coxale nettement allongée antéro-ventralement, et un 2e uropode à branche interne non étranglée et porteuse de courtes épines. *Anonyx compactus* est plus petite (12–17 mm), porte une épine ventrale assez longue sur chacun des deux premiers articles du flagellum de la 1e antenne, un angle délimitant la 3e plaque latérale du métasome de son prolongement pointu postérieur, un 1e péréiopode fortement parachéliforme et à bord palmaire perpendiculaire, et un 2e péréiopode assez fortement subchéliforme. *Anonyx sarsi*, de taille moyenne (20–31 mm), porte au labre une crête médiane de proéminence et hauteur minimales et, sur la branche externe du 2e uropode, des épines assez uniformément courtes sur les deux tiers proximaux du bord interne (pas d'épines chez *laticoxae* et *compactus*); chez la femelle, le bord dorsal du 4e article pédonculaire de la 2e antenne porte des touffes plutôt qu'une rangée de soies, mais l'espèce est par ailleurs morphologiquement semblable à *Anonyx nugax*.

Les cinq autres espèces sont caractérisées par une rangée de paires de longues soies au bord postérieur du 6e segment des 3e et 4e péréiopodes et, sauf chez *nugax*, par un labre à lobe assez proéminent. Sauf chez *ochoticus* et *lilljeborgi*, le 2e uropode porte des épines au bord interne de sa branche externe. *Anonyx ochoticus*, la plus petite espèce (9–10 mm), porte sur le 1e segment de l'urosome une crête dorsale surplombant nettement les segments postérieurs. *Anonyx debruyni*, assez petite (15–21 mm), possède un 1e péréiopode parachéliforme à bord palmaire oblique, un 2e péréiopode très fortement subchéliforme, un labre et un lobe céphalique latéral des plus proéminents et étroits et, sur la branche externe du 2e uropode, seulement deux petites épines dans la moitié distale du bord interne. *Anonyx lilljeborgi*, de petite taille (9–18 mm), porte au labre la languette la plus proéminente, d'ordinaire régulièrement et largement arrondie, un bord céphalique ventral concave (comme chez *debruyni*), et une 2e plaque latérale du métasome dont le coin postéro-ventral est presque dépourvu de dent. *Anonyx nugax* est la plus grande espèce (31–44 mm), son labre est peu proéminent, le coin postéro-ventral de la 2e plaque latérale du métasome porte une dent bien évidente, tandis que la 3e porte au même coin un prolongement pointu court et à bord postéro-ventral presque dépourvu de concavité, et la branche externe du 2e péréiopode porte sur son bord interne une rangée d'épines de tailles assez semblables, absentes dans le tiers distal de la branche. *Anonyx pacificus* est aussi de forte taille (27–34 mm) et semblable à *nugax*, dont elle diffère par son labre à proéminence plus prononcée et angulaire, par le prolongement postérieur — plus long et plus distinctement concave ventralement — de la 3e plaque latérale du métasome et, au bord interne de la branche externe du 2e uropode, une rangée d'épines de tailles distalement croissantes, présentes dans le tiers distal de la branche.

Trois espèces, *nugax*, *lilljeborgi* et *sarsi*, ont une distribution circumpolaire arctique-boréale, *sarsi* habitant surtout les faibles profondeurs (<50 m). Quatre espèces (*pacificus*, *laticoxae*, *ochoticus* et *compactus*) sont des formes d'eau plus froide présumément d'origine pacifique et toutes nouvelles pour l'Atlantique nord. La distribution de *debruyni* est incertaine.

INTRODUCTION

Among the amphipod Crustacea of the Arctic and Atlantic coasts of Canada and the northeastern United States, those of the family Lysianassidae, and

especially of the genus *Anonyx*, are important in the economy of the sea, both as fish food and as predators of dead, weakened, or perhaps simply trapped fish or other large marine animals of actual or potential commercial interest. These amphipods are very frequently encountered and often occur in large concentrations on and in their common prey, which they can clean to the skeleton in a few hours (Parry, 1824; Goës, 1866; Scarratt, 1965; Shave, 1966; P. Brunel, unpublished observations).

During a study of the reproductive cycles of amphipods from collections made by the M.V. *Calanus* in Canadian eastern Arctic waters (Steele, 1961), it was observed that specimens then identified as *Anonyx nugax* (Phipps) were mature at a wide range of sizes. Stephensen (1923) had reported similar observations in his study of the *Ingolf* collections. However, a closer examination of the *Calanus* specimens revealed that the forms which differed in their size at maturity also varied consistently in their morphology. At that time these forms were regarded as undescribed species. Since the junior author had also found them in collections from the Gulf of St. Lawrence, we have agreed to publish jointly the results of our investigations. Our study has now been greatly expanded and an attempt made to revise most of the available material from the northwestern Atlantic and to examine all of the type-specimens in the genus *Anonyx* that could be found. This analysis has modified many of our earlier ideas concerning the status of our "new" species and has led to the discovery of additional undescribed species.

While this work was in progress, Gurjanova (1962) published an account of the *Anonyx* species of the northern Pacific in which she described as new several of the forms that we had found in the northern Atlantic. However, without examining the available type-specimens, she has also made some understandable errors in her determinations. More recently Hurley (1963) has described two other new species from the west coast of North America and discussed the taxonomy of the genus as a whole.

The present paper is an attempt to provide in a single source a means for identifying the species of *Anonyx* which occur in the area selected for study, which extends from the arctic border of Alaska eastward to western Greenland and southward to the limit of distribution of the species off the American coast. This objective, as well as the inadequacy of most previous descriptions and figures, required new descriptive and pictorial information. This has been done for mature specimens — the females being given the fuller treatment — as well as for positively identified very young individuals, which have been the source of much taxonomic confusion in the past and are systematically ignored as such in taxonomic works.

Because of this past neglect to give their due importance to growth stages, and also because of the superficial similarity of all the species, the literature on the old genus *Anonyx* is extensive and strewn with problems of nomenclature. The review of previous work is accordingly given at the end of our paper in the form of an annotated chronological bibliography, in which we include some discussion of species not found in the selected area.

Our extensive revision of past identifications has rendered obsolete practically all previous knowledge on geographic distribution of the species. It was therefore necessary to prepare new distribution maps, which are given in the present work, and from which meaningful patterns have provided an opportunity to draw some preliminary zoogeographic conclusions.

MATERIALS AND METHODS

The present study is based on the examination of 5585 specimens contained in 814 samples from almost as many localities. The extent of sampling for each species is summarized in Table IX. Detailed collecting data pertaining to all specimens examined, the museum reference of the samples, and the numbers of individuals are available in Technical Report No. 47 of the Fisheries Research Board of Canada.

An attempt was made to revise most of the available material from the northwestern Atlantic and to this end all of the specimens from this area in the following institutions were examined: United States National Museum; Arctic Biological Station (Fisheries Research Board of Canada); Station de Biologie marine (Quebec Fisheries Division); U.S. Bureau of Commercial Fisheries Biological Laboratory at Woods Hole; Zoological Museum of the University of Copenhagen; and Royal Ontario Museum of the University of Toronto. In addition, all of the *Anonyx* material in the British Museum (Natural History), the Muséum National d'Histoire Naturelle in Paris, and the National Museum of Canada was studied. A special effort was made to obtain collections from the southern end of the range of the genus along the east coast of the United States south of Cape Cod. Several laboratories in recent years have made surveys of the bottom fauna in this area, but the material is not yet well represented in the sorted collections of the United States National Museum. Since few *Anonyx* specimens were obtained from these East Coast laboratories, one may assume that the southern limit of the genus is fairly well established by the available specimens.

Collections from outside the area of study were examined only incidentally in the course of this study or because of a special interest, e.g. they were of large size, came from great depths, or had a controversial status from previous studies. Records from outside the area of study are given only when we have examined the specimens. A special effort was made, however, to locate and examine the types of all described species, in order to study them critically and to compare them with specimens from the northwestern Atlantic. Details of this search are given in the text.

Our descriptions and illustrations of the species are based mainly on mature female specimens from the northwestern Atlantic, except for *Anonyx laticoxae*, of which we had not found a mature female. The largest and most suitable specimen of this species came from the Bering Sea.

The specimens were examined intermittently over a period of several years, during which time we discovered new characters of diagnostic value. Since time did not allow a re-examination of the entire collection after our

new ideas had become settled, we cannot claim to have checked on every specimen all the characters described below. In such cases we checked them on a small sample of animals from different geographic localities, and we assumed that the original combination of characters which had enabled us to distinguish the species in the first place was always associated with the new characters as it was on the fewer specimens which we observed. This extrapolation was of course unavoidable for characters of the mouthparts requiring dissections and slide preparations: the latter had to be kept to a minimum because of time limitations.

Specimens for dissection were usually stained in Chlorazol Black E, cleared in a saturated KOH solution if they were of large size, and all the appendages of one side, plus the metasome lateral plates, the telson, and a few appendages of the other side were mounted in Turtox CMC-10 (or CMC-S if not already stained) mounting medium. The specimens used for the drawings were preserved. Length measurements were made from the anterior margin of the head to the end of the telson, with the animal in an extended position.

There is no consistency in the terminology applied to the thoracic appendages of the Malacostraca in the literature. This is due to the great variation in the structure and function of these appendages and the amount of fusion of the anterior thoracic somites with the head. This confusion has been discussed in some detail by Gordon (1960).

Three types of thoracic appendage are commonly distinguished — maxilliped, gnathopod, and peraeopod. However, the criteria used to distinguish them vary with different authors so that the same appendage may be referred to with different names. The maxilliped is modified for chewing and filtering of food and possesses endites (Siewing, 1958, quoted in Gordon, 1960). The gnathopod is a leg modified as a grasping organ and is usually chelate or subchelate. The unmodified walking legs which follow are often referred to as peraeopods. However, this has led to confusion because the free somites of the thorax comprise the peraeon. Thus the appendages on these somites become the peraeopods. "Peraeopod is not by derivation a walking leg but an appendage of any one of the peraeon somites." (I. Gordon, personal communication). Therefore, although it is correct to name "gnathopods" the modified anterior peraeopods, it is not correct to number the following peraeopods beginning with one.

There is much to be said for numbering all thoracic appendages (thoracopods) from one to eight in all of the Malacostraca as is done by Tattersall and Tattersall (1951) and Gordon (1960) for mysids. They could then be described as maxilliped, gnathopods, or walking legs without reference to what somite they arise from. However, present usage in the amphipods employs either the maxilliped, peraeopod 1–7 or the maxilliped, gnathopod 1–2, peraeopod 1–5 terminology. Since the latter is incorrect, the maxilliped, peraeopod 1–7 system is used in this paper.

The segments of the peraeopods are referred to by number.

The preparation of the illustrations has been shared as follows between the two of us: Fig. 4–17, 20–23, 26–28, 31–49 and 52 were prepared by the senior author, using a camera lucida to draw the whole animal, and microprojection apparatus for the dissected parts; the remaining drawings are the work of the junior author using only the microprojection apparatus.

The synonymy of each species has no pretension to exhaustiveness: it lists all different names known to us, in their first application to the species, and later uses of these names only when they are included in publications of taxonomic significance because of the presence of figures, new or inclusive descriptive information and keys, or misidentifications. Several references are omitted in which the species cannot be identified with some confidence. These references are cited in the annotated bibliography.

GENUS *ANONYX* KRØYER, 1838

Synonymy

Chironesimus G. O. Sars, 1891, p. 108; *Lakota* Holmes, 1908, p. 498.

The definition of the genus *Anonyx*, originally given by Krøyer (1838a), has been progressively amplified by Boeck (1872), Sars (1891), Stebbing (1906), Gurjanova (1951, 1962), and Hurley (1963). The degree of variation within the genus has been disclosed by the recent description of many new species from the Pacific by Gurjanova (1962) and Hurley (1963). We have only a few modifications to add and present the following definition of the genus.

Definition

Body stout, with well-developed appendages. Head with a very small rostrum and prominent rounded interantennal lobes. Eyes large, dark, and usually expanded below. First segment of the peduncle of antenna 1 usually carinate on the dorso-medial edge and slightly projecting anteriorly. Upper lip separated from the epistome by a deep sinus and variably produced in front of the epistome into a laterally compressed median keel or lappet. Mandibles elongate, with a well-developed palp situated anterior to and above the molar; cutting edge with teeth; molar well developed, obliquely conical, and covered with hair; left mandible with a blunt, elongated *lacinia mobilis* near the cutting edge. Maxilla 1, inner lobe with two long plumose setae; outer lobe truncate, and bearing 11 strong denticulate spines; apex of palp with socketed teeth. Maxilla 2 with short broad lobes, inner usually about one-half of the length of the outer, hairy and bearing one long and a series of shorter spiniform plumose setae on the apex and inner margin; outer lobe with a series of pectinate spine-setae, and plain spine-setae on the inner margin and apex. Lower lip hairy, without inner lobes. Maxilliped, inner lobe short and armed with plumose setae near the distal and inner margins; outer lobe broad, not reaching the distal end of the second segment of the palp, distal and inner margin weakly dentate; palp strong. Peraeopod 1, coxal plate usually expanded antero-distally, not tapering distally; palm transverse or oblique and defined by one to three stout spines; dactyl strong. Peraeopod 2 long, subchelate, or minutely chelate; dactyl variable in size. Peraeopods 3 and 4 with a short blunt spine at the posterior distal corner of segment 6. Peraeopods 6 and 7 subequal, both longer than peraeopod 5. Branchial vesicles present on the coxa of peraeopods 2–7; those of peraeopods 2–6 transversely pleated in large specimens but generally unpleated in small ones; those of peraeopods 7 unpleated; those

of peraeopods 3 and 4 with a small accessory lobe. Metasome segment 3, lateral plate[4] produced into a large posterior projection. Urosome segment 1 dorsally carinate and projecting posteriorly to a varying degree. Uropod 2, inner ramus unconstricted with short spines, or constricted to a varying degree, with a longer spine at the level of the constriction. Uropod 3, rami projecting beyond uropods 1 and 2, and usually equipped with plumose setae on at least the inner margins. Telson elongated and deeply cleft.

Other Probable Generic Characters

In addition to the characters embodied in the definition of the genus *Anonyx* which is given above, other characters are found in all the species which we have examined, including some which are not illustrated in the present paper, and in published illustrations of other species. The characters should probably be incorporated into the generic definition of *Anonyx*, but we prefer here to set them aside until the other species have been more thoroughly examined. We are aware that several of these characters occur in other lysianassid genera, and it is conceivable that some may even prove to apply to the entire family. But we have the impression that they generally do so in different combinations in the various genera, and that therefore they should be explicitly described or illustrated in future descriptions of new or ill-known species of Lysianassidae. Only in this way will the present extensive generic confusion eventually be eradicated from this family.

Sculpturing of integument.—Large species have a pebble-grain surface structure. All species apparently possess scattered pit-like impressions or pores.

Antenna 1.—The first segment of the peduncle is carinate medially and projects slightly anteriorly; its dorsal and medio-ventral edges bear rows of feathery setae. The first segment of the flagellum is usually shorter than, and seldom as long as, the first segment of the peduncle, and its inner flattened surface (which matches with the flattened and enlarged first segment of the accessory flagellum) is covered with a series of brushes or setae arranged in transverse rows grouped in two longitudinal fields joining each other proximally. The insertions of the brushes are marked by peculiar geometric refringent patterns arranged in longitudinal pairs forming the transverse rows, giving the whole area the appearance of a rasp. In addition, the inner distal margin of the first flagellar segment may bear ventrally, at least in the adults of the large species, some very small and blunt rods, which are possibly homologous with the several long "flaccid sensory setae" noted and figured on the same segment by Hurley (1963) for the following species: *Aristias veleronis*, *Lepidepecreum* (2 species), *Uristes californicus*, "*Anonyx*" *adoxus*, and *dorotheae* (which we suspect are not *Anonyx*), *Orchomenella decipiens*, and *Hippomedon zetesimus*. Hurley's flaccid sensory setae are obviously aesthetascs, the so-called olfactory rods,[5] described in amphipods (Leydig, 1878; Blanc, 1884) and most other crustacean orders as being especially abundant on antennules and antennae. In none of the *Anonyx* species which we examined are these aesthetascs long and conspicuous. They are in fact very difficult to see. In *Anonyx compactus*, there is one long and acute spine at the distal corner of the first flagellar segment, but it is really a spine, probably homologous with the still longer spine figured by Hurley (1963) for "*Anonyx*" *dorotheae*, which is otherwise well supplied with conspicuous examples of the distinct aesthetascs. In *Anonyx* as well as in other species figured by Hurley, aesthetascs also occur in other segments of the flagellum and on the last peduncular segment, without obvious orderly disposition to our present knowledge.

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[4]The expression "epimeral plate" is still used in the amphipod literature, despite Calman's advice (in Lankester's "Treatise of Zoology," 1907) that "pleuron" should replace "epimeron." "Pleural plate" not being used for amphipods to our knowledge, it seems better to retain the alternative and anatomically noncommitted "lateral plate."

[5]The chemoreceptive function of these aesthetascs, although not yet traced with definite assurance to the structure itself, is suggested by the work of Laverack (1964).

Epistome.—The epistome is not projecting, and it is closely adjacent to the upper lip, from which it is marked off by a very tightly closed sinus.

Maxilla 1.—The outer lobe has a distal hairy area, and a proximal tuft of longer hair, and 2 of its 11 denticulated spines are separated from the others by a space and located close to the hair tuft. The denticulated spines bear from 1 to 9 accessory teeth. The palp is distally broadened but not markedly curved, the distal part of its inner edge is not serrated, and its distal edge is weakly convex. This latter edge is bordered by 6–10 symmetrically conical socketed teeth without any serrated or denticulated edge, an inner unsocketed tooth, and usually a hair between the outer 2nd and 3rd teeth.

Maxilliped.—The inner lobe bears, on the medial half of its distal margin, three nodular teeth separated by two spaces. The distal medial corner forms a right or obtuse, but not an acute, angle and the distal edge is not concave. The outer lobe is bordered medially and distally with very small nodular spines (or socketed nodules) — called "taste cylinders" by Grimm (1880) — none of which is much larger or longer than the others. The edge may be more or less scalloped, but its general contour is very broadly rounded and nowhere angular,[6] and there is no parallel row of slender spines on the surface of the plate.

Peraeopod 1.—The palm of segment 6 is bordered with crowded slender and acute denticles which usually make a continuous row along the entire palm. (The row may border only the anterior half of the palm in *A. debruyni*; we do not know how commonly it does so, however.)

Peraeopods 1–4.—The first three coxal plates have, at their postero-distal corner, a small notch in which is inserted a small hair. (Because of its small size, this notch does not usually appear on drawings, including some of ours.) The distal edge of the first four coxal plates is not setose.

The dactyl of peraeopods 3–4 is curved and fairly acute, slender distally, and swollen proximally. Its length is contained between 1.8 and 2.3 times (mean: 2.03, N = 16) in the length of segment 6 in mature specimens, and a little less, between 1.6 and 2.3 times (mean: 1.87, N = 11) in young specimens 2.3–10 mm long.

Peraeopods 5–7.—The anterior margin of peraeopods 5 and 6, especially that of segment 4, is supplied with spines and setae, whereas on peraeopod 7 there are only spines. Segment 4 of peraeopods 5–6 furthermore has a convex hind margin, whereas on peraeopod 7 this margin is straight or nearly so.

Urosome segment 3.—There is one minute dorsal spine on either side of the segment, above the insertion of the telson.

Uropods 1–2.—The tip of each ramus is armed with a stout embedded "spine" (called "integral spine" by Hurley, 1963), only a third or a quarter of which protrudes outside into a blunt, more heavily sclerotized, often curved and sometimes pimpled knob, which may well be homologous with the ungus at the tip of the dactyl of the peraeopods.

Variation with Species, Sex, and Size

Our examination of specimens from the northwestern Atlantic, as well as the work of Gurjanova (1962) and Hurley (1963), indicate that throughout the genus there is considerable stability in most characters, but particularly in mouthparts. The reliance on mouthparts to distinguish species explains why considerable confusion has existed concerning the status of several old species and why other common forms have not been recognized until recently. The genus is actually quite variable in other characters: shape of the head, size of the eye, shape of the upper lip, shape of the first peduncular segment of antenna 1, details of the armature of the mouthparts, size and angle of

[6]Some published figures of the contour and armature of the outer plate, such as Gurjanova's (1962) fig. 85B of *Anonyx eous*, of which we have examined a specimen, may be inaccurate in this respect.

the palm of peraeopod 1, shape of segment 6 and size of the dactyl of peraeopod 2, armature of the sixth segment of peraeopods 3 and 4, relative size and serrations of the second segment of paraeopod 7, shape of the lateral plates of metasome segments 2 and 3, and shape and armature of the uropods. These structures have been most useful in distinguishing the species.

As in other amphipods there are variations in morphology with sex and size, and these often make specific determinations difficult. Mature male and female *Anonyx* resemble each other closely in general appearance but differ notably in several characters.

The mature male is distinguished by longer antennae equipped with calceoli. The second antenna is extremely long, extends to the metasome, and is apparently carried by the mature male inside the coxal plates of the peraeopods. The elongation is due to an increased number of segments and to the greater length of the distal segments. The increase in the number of segments becomes apparent as soon as the copulatory papillae appear and continues as the animal grows, whereas the extension of the individual segments, which causes a sudden increase in the length of the antennae, and the development of calceoli, take place in one moult. Another sexual difference, more obvious in some species than in others, is the slightly larger size of the eye of the male. In two species, *A. sarsi* and *A. nugax*, moreover, some mature males have the eyes still more enlarged (see Fig. 18A), which indicates the existence of two sorts of males, one nearly resembling, the other very different from, the females, as observed long ago by Sars (1871) in four orders of Crustacea. Simultaneously, in some species the male uropods may develop a characteristic armature. There may be in effect a miniature metamorphosis as the animal attains maturity. Similar transformations have been observed in other male amphipods, most notably in *Pontoporeia affinis*, studied in great detail by Segerstrale (1937, 1950), where the changes are related to a vertical migration and swarming behaviour which takes place during mating in the winter. The mature males are found only at this time. The morphological changes in *Anonyx* suggest that they may have a similar behaviour, and the occurrence of the mature males of some species (e.g. *A. nugax* and *A. lilljeborgi*) in the plankton gives added support to this view. In addition, the narrow size-range of mature males found in any one area suggests that they do not live long or moult after attaining maturity, even though the mouthparts do not degenerate and the animals apparently feed. On the other hand, mature males of the common species occur during most of the year, suggesting that there may be a long breeding season.

Mature females, recognized by the possession of long oostegites bearing long setae, are uncommon in collections of most species, and like the males have a narrow size-range in any area. As none of the females seen could be considered to be in a resting stage, it seems probable that they also have a short life and do not moult after producing a single brood.

The difficulty of assigning diagnostic value to characters which are modified with growth, maturity, and sex, such as the length and number of

segments of the antennae, has led us to abandon such characters to distinguish the species of *Anonyx*. This difficulty does not mean, however, that there is no such value in these characters. It is only that we do not have yet any refined morphometric data which have been made independent of size and sex. In fact, we suspect that there is still such value in the antennae: *A. laticoxae*, *sarsi*, *lebedi*, *dalli*, for instance, appear to have either a shorter first antenna or a shorter first flagellar segment, than others like *nugax*, *pacificus*, *debruyni*, *compactus*, and *ochoticus*.

Gurjanova (1962) has described differences in the structure of peraeopod 2 for the males and females of some species, which could not be found in our specimens from the northwestern Atlantic (e.g. *A. debruyni*), and it is suspected that she has included more than one species in her determinations.

The genus *Anonyx* is now known to contain a number of species that mature at sizes ranging from 8 to 45 mm (measured from the anterior edge of the head to the distal end of the telson). The small species noticeably resemble similar-sized young of the larger forms, and the young of all species are not easily distinguished. Many characters that are distinctive on the large specimens, such as the shape of the head and of the eye, the absence of an accessory tooth on the dactyl of peraeopod 1, the relative length of the rami of uropod 3 and of the distal segment of the outer ramus, the degree and type of armature of the uropods, and the shape of the lateral plate of metasome segment 3, are useless for determining small specimens. Therefore, it is often difficult to identify the young and apparently on several occasions they have been described as a species different from the adult. It is for this reason that the young are also described in the present paper.

A further difficulty arises with those species which extend over a wide range of latitude and live in a variety of conditions. The northern specimens tend to mature at larger sizes, and although they are readily identified, they usually have a better-developed armature of spines, setae, serrations, and other meristic characters, in accordance with their larger size.

Discussion of Generic Synonymy

The synonymy of *Lakota* with *Anonyx* has been suspected for a long time (Barnard, 1925; Schellenberg, 1926; Gurjanova, 1962) and was formally proposed by Hurley (1963). It is confirmed here since our examination of the holotypes of *Lakota carinata* Holmes, 1908, the type-species, and of *Lakota chelata* Chevreux, 1926, has shown that these specimens are respectively identical with *Anonyx lilljeborgi* Boeck, 1870 and *Anonyx nugax* (Phipps, 1774). Furthermore, we have found that the other species assigned to the genus *Lakota*, *L. adversicola* and *L. rotundatus* K. H. Barnard, 1925, are in fact entirely different from the genus *Anonyx*. On the other hand, the transfer of *Lakota* into the synonymy of *Chironesimus* (Schellenberg, 1926; Barnard, 1940) did not involve the type-species and was not supported by an examination of the insufficiently described and illustrated type-specimen.

The genus *Chironesimus* was fused to *Anonyx* by Gurjanova (1962) on the basis of her discovery that its diagnostic characters were shared with several other newly described species of *Anonyx*, or were simply part of a series exhibiting all degrees of expression within the genus. We accept here Gurjanova's action. However, there are indications that *Chironesimus*, together with species of the *compactus–oculatus* group, stands at one end of the spectrum of specific variation within the genus. The characters of this group of species, which might conceivably become a subgenus when we have better knowledge, might combine as follows:

Antenna 1.—First segment of flagellum rather elongated and better supplied with sensory setae or elongated spine(s).

Peraeopod 1.—(*a*) Coxal plate not expanded antero-distally; (*b*) palm short, transverse or oblique (i.e. parachelate or weakly subchelate), marked off from the hind edge of segment 6 by more than the usual two spines; (*c*) hind edge of segment 6 with spines in its distal part.

Peraeopod 2.—Palm and dactyl longer than in the other species (i.e. strongly subchelate).

Peraeopod 7.—Second segment rather large, about as long as or longer than the distal rest of the limb.

Uropod 2.—Inner ramus well constricted, with a long spine thereon.

Key to the Species of *Anonyx* in the Northwest Atlantic

A. Posterior edge of sixth segment of peraeopods 3 and 4 with a single row of long setae and a corresponding row of spines.

B. Uropod 2, inner ramus not constricted and bearing on the inner edge a short distal spine (equal in length to one-seventh of the distance from the insertion of the spine to the end of the ramus). Spines on peraeopods 3 and 4 short and thick. . . . *Anonyx laticoxae* Gurjanova

BB. Uropod 2, inner ramus constricted and bearing at the point of the constriction a long spine (equal in length to one-quarter to three-quarters of the distance from the insertion to the end of the ramus). Spines on peraeopods 3 and 4 long and slender.

C. Uropod 2, inner ramus completely constricted distally and bearing at the point of constriction a long spine (equal in length to three-quarters of the distance from the point of insertion to the end of the ramus). . . . . *Anonyx compactus* Gurjanova

CC. Uropod 2, inner ramus only partly constricted, with the spine at the point of the constriction equal in length to one-quarter of the distance from the insertion to the end of the ramus . . . . . *Anonyx sarsi* n.sp.

AA. Posterior edge of the sixth segment of peraeopods 3 and 4 with a row of pairs of long setae and a few short setae and/or spines.

D. Uropod 2, inner ramus completely constricted and bearing at the point of constriction a long spine (equal in length to one-quarter to three-quarters of the distance from the insertion to the end of the ramus) . . . . . *Anonyx ochoticus* Gurjanova

DD. Uropod 2, inner ramus only partially constricted, spine at the constriction shorter (usually equal to or shorter than one-half the distance from the insertion to the end of the ramus).

E. Segment 6 of peraeopod 2 expanded distally, palm and dactyl larger than those of peraeopod 1. . . . . *Anonyx debruyni* Hoek

EE. Segment 6 of peraeopod 2 not expanded distally, palm and dactyl smaller than those of peraeopod 1.

F. Lateral plate of metasome segment 2 not produced at the lower posterior corner into a conspicuous tooth. Without spines on the inner edge of the outer ramus of uropod 2. . . . . *Anonyx lilljeborgi* Boeck

FF. Lateral plate of metasome segment 2 produced at the lower posterior corner into a conspicuous tooth. With spines on the inner edge of the outer ramus of uropod 2.

G. Uropod 2, inner ramus constricted just beyond the middle; outer ramus, distal third of inner edge without spine. Posterior projection of the lateral plate of metasome segment 3 produced into a short point. Upper lip scarcely extending in front of the epistome. ..... *Anonyx nugax* (Phipps)

GG. Uropod 2, inner ramus constricted well beyond the middle; outer ramus, distal third of inner edge with at least one spine (specimens >9 mm). Posterior projection of the lateral plate of metasome segment 3 produced into a long point. Upper lip extending well in front of the epistome. .... *Anonyx pacificus* Gurjanova

This key should be suitable even for small specimens, but may be difficult to apply to the small *A. sarsi*, *nugax*, *pacificus*, and *lilljeborgi* which look very much alike. In the young of the latter three species the inner setae on the hind edge of segment 6 of peraeopods 3 and 4 are shorter than the outer and could be mistaken for slender spines. The difference is apparent under high magnifications.

In case of difficulties of identification, for instance when specimens lack diagnostic parts, and to save a lengthy search through the descriptions, there are two recources: (1) the abstract and the résumé contain a kind of abridged "key" using other characters of adults; (2) we have prepared for each species a diagnosis isolating a still larger series of those characters which are especially useful to make the identification. It should be understood that a character which is mentioned for one or some species and not for others is lacking in the latter.

DESCRIPTIONS OF THE SPECIES

Anonyx nugax (Phipps, 1774)

SYNONYMY

Cancer nugax Phipps, 1774, p. 192, pl. XII, fig. 2.

Gammarus nugax — J. C. Fabricius, 1781, p. 515.

Talitrus nugax — J. C. Ross, 1826, p. 119.

Atylus nugax — Latreille, 1829, p. 120.

Lysianassa Lagena Krøyer, 1838a, p. 237, pl. I, fig. 1.

Lysianassa appendiculosa Krøyer, 1838a, p. 240, pl. I. fig. 2.

Anonyx Lagena Krøyer, 1838a, p. 244 (not *A. lagena* — Sars, 1895, p. 686; Stebbing, 1906, p. 54).

Anonyx appendiculosus Krøyer, 1838a, p. 244.

Lysianassa appendiculata — Milne-Edwards, 1840, p. 21; Bate, 1862, p. 67, pl. X, fig. 8.

Anonyx ampulla — Krøyer, 1845, p. 578; Krøyer, 1846?, pl. 13, fig. 2; Krøyer, 1846, p. 43 (not *A. ampulla* — Bate, 1862, p. 79, pl. XIII, fig. 5) (not *Cancer ampulla* Phipps, 1774, p. 191 pl. XII, fig. 3).

Lycianassa lagena — Bell, 1855, p. 406.

Anonyx lagena (part) — Bate, 1862, p. 77, pl. XII, fig. 7; Boeck, 1870, p. 28; Boeck, 1872, p. 152; Heller, 1875, p. 29, pl. I, fig. 6–15.

Anonyx ampulloides Bate, 1862, p. 78, pl. XII, fig 8 (not *A. ampulloides* — Stebbing, 1888, p. 608, pl. III; Gurjanova, 1951, p. 225, fig. 90; Gurjanova, 1962, p. 271, fig. 88A–B; Nagata, 1960, p. 166, pl. XIII, fig. 1–6).

Lysianassa Fisheri Lockington, 1877, p. 48.

Anonyx nugax — Miers, 1877a, p. 135.

Anonyx kukenthali Vosseler, 1889, p. 154, pl. VIII, fig. 1–17.

Anonyx nugax (part) — Sars, 1891, p. 88, pl. 31; Stebbing, 1894, p. 7; (?) Holmes, 1904, p. 313, pl. XXXV, fig. 17–19, pl. XXXVI, fig. 20; Stebbing, 1906, p. 54; Brüggen, 1907, p. 216; Stappers, 1911, p. 8; Stephensen, 1923, p. 78; Stephensen, 1935, p. 64; Gurjanova, 1951, p. 222,

fig. 87; (?) Gurjanova, 1962, p. 216, fig. 67A–B (not *A. nugax* — Holmes, 1905, p. 472, 1 fig., pl. III, fig. 3; Shoemaker, 1930b, fig. 1; not *A. nugax pacificus* Gurjanova, 1962, p. 219, fig. 68A–B, 69A–B).

Lakota chelata Chevreux, 1926, p. 9, fig. 5; Stephensen, 1935, p. 88, fig 13.

Lacota chelata — Gurjanova, 1951, p. 261, fig. 131.

DIAGNOSIS OF MATURE FEMALE

Large, upper lip slightly produced in front of the epistome, segment 6 of peraeopod 1 narrowed only slightly distally, dactyl without an accessory tooth, dactyl of peraeopod 2 small, hind edge of segment 6 of peraeopods 3 and 4 with a row of pairs of long setae and a few unpaired slender spines, segment 2 of peraeopod 7 prominently and coarsely serrated on distal hind edge, shorter than rest of the limb, inner ramus of uropod 2 constricted just beyond the middle and bearing a medium-sized spine at the level of the constriction, inner edge of outer ramus with small spines not extending into the distal third of the ramus, second metasome lateral plate with a distinct tooth in the postero-ventral corner, posterior projection of the third metasome lateral plate short and produced into a blunt point.

DESCRIPTION OF MATURE FEMALE

This is one of the largest species of *Anonyx*, which reaches maturity at a length of 31–44 mm.

Head.—Shorter than the combined length of the first two segments of the mesosome. Interantennal lobe right-angled, but a little rounded, more so than in *A. pacificus*, lower margin straight. Eye large, broad and expanded ventrally to occupy most of the interantennal lobe, posterior edge concave, dark brown or black in colour.

Antenna 1.—Peduncle shorter than the head, large; first segment longer than it is high, dorsal profile almost straight. Flagellum short, with pairs of short rods (aesthetascs) on the medial surface of the first four segments of the flagellum and third segment of the peduncle.

Antenna 2.—Fourth segment of the peduncle with an inner row of feathery setae and an outer row of long setae on the lower edge, and a row of short setae on the dorsal edge. Four tufts of setae and a row of feathery setae on the lower edge and a dorsal row of short setae on the fifth segment of the peduncle. Flagellum short, with long ventral setae.

Upper lip.—Projecting only slightly in front of the epistome as an evenly rounded lobe.

Right mandible.—A single prominent tooth on the cutting edge. Three spine-teeth and three to five hairy setules in the spine row. Palp, second segment cylindrical and slightly longer than the third; the latter hairy on the anterior surface and with plumose coarse setae on the posterior margin.

Left mandible.—Two teeth on the cutting edge.

Maxilla 1.—Outer lobe bearing six broad spines with one to two accessory teeth and five long spines each without or with only one accessory tooth. Palp distally expanded and bearing eight acute conical socketed teeth on tall widely spaced stalks.

Peraeopod 1.—Coxal plate setose medially, expanded anteriorly as a rounded lobe, its maximal width shorter than the height below the antero-proximal corner. Segment 6 equal in length to segment 5, narrowed only slightly distally, palm perpendicular, and defined by two stout spines. Dactyl slightly longer than the palm, without an accessory tooth.

Peraeopod 2.—Sixth segment short, half as long as fifth, covered distally and ventrally by long setae with a forked tip and a pectinate medial margin; palm slightly concave, finely denticulate, produced slightly under the small dactyl which is setose and distally pectinate and denticulate on the inner margin.

Peraeopods 3 and 4.—Posterior margin of segment 6 with a row of pairs of long setae and a few elongated spines, the latter not paired with the long setae; blunt spine at the posterior lower corner of segment 6 only slightly hooked and lacking an accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with more than 20 serrations, those of the distal half distinctly more crowded and prominent than the proximal ones; maximal length of the segment distinctly shorter than the rest of the limb.

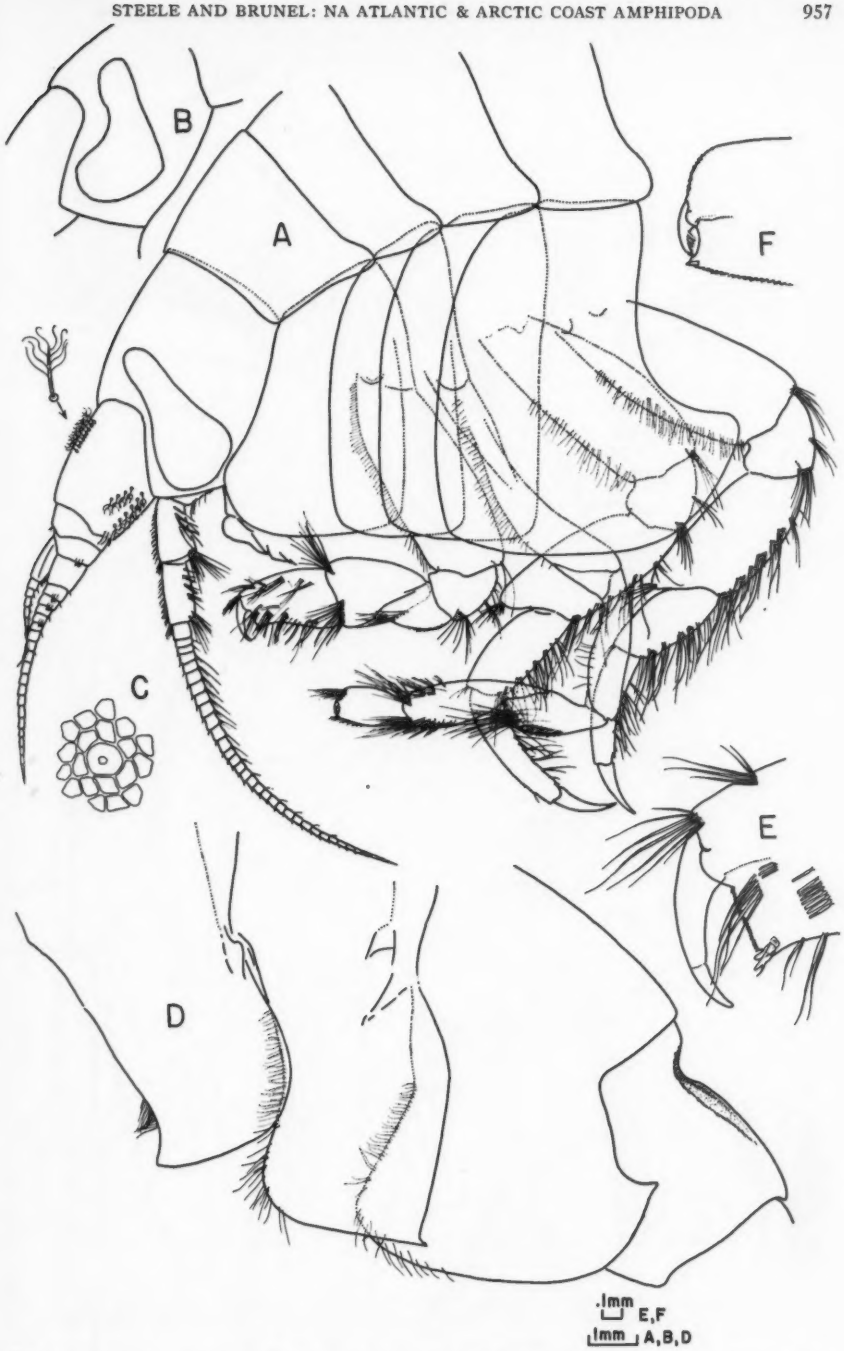

FIG. 1. *Anonyx nugax* (Phipps). A, C–F, mature female, 41 mm, St. Lawrence Estuary, D 36. A, anterior; C, sculpturing; D, metasome; E, peraeopod 1; F, peraeopod 2; B, head of mature male, 40 mm, St. Lawrence Estuary, D 36.

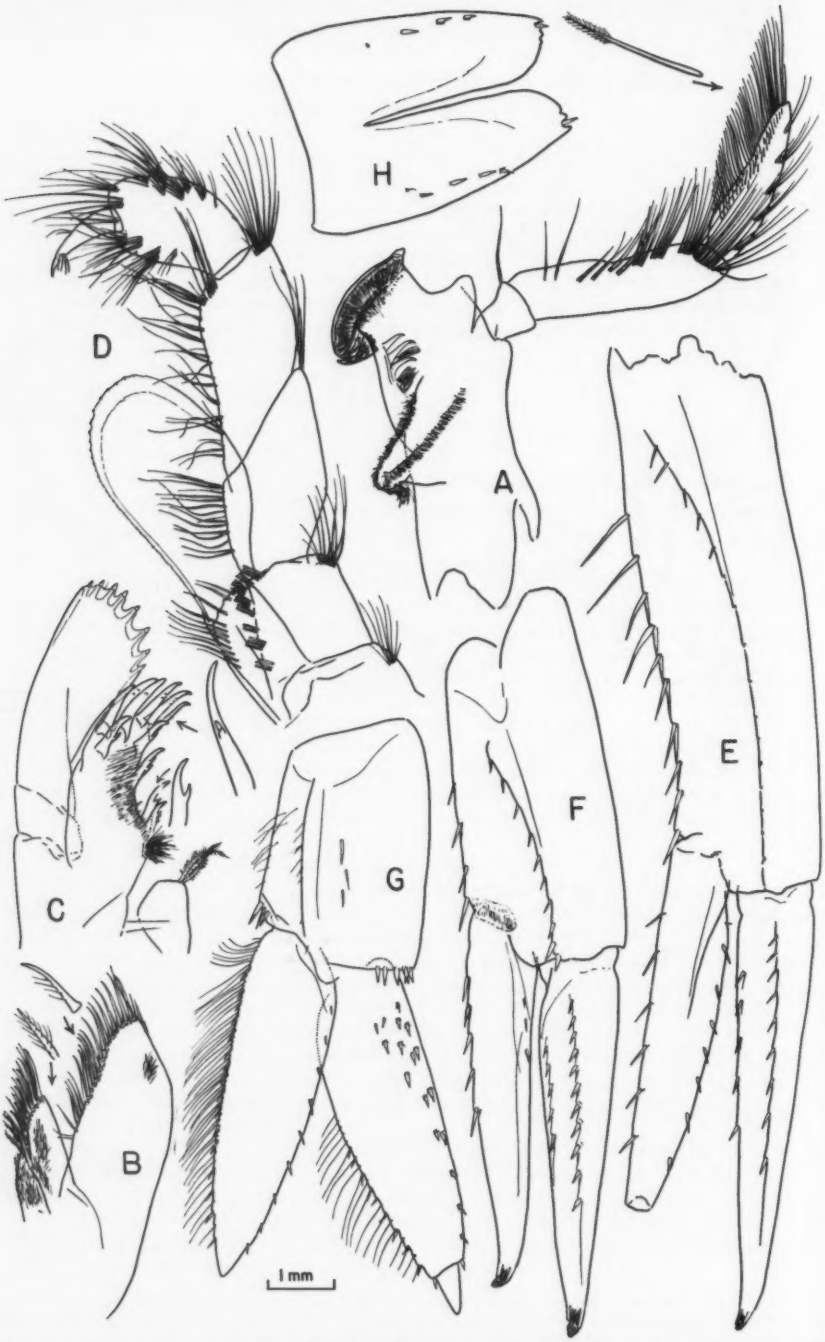

FIG. 2. *Anonyx nugax* (Phipps). Mature female, 41 mm. St. Lawrence Estuary, D 36. A, right mandible; B, maxilla 2; C, maxilla 1; D, maxilliped; E, uropod 1; F, uropod 2; G, uropod 3.

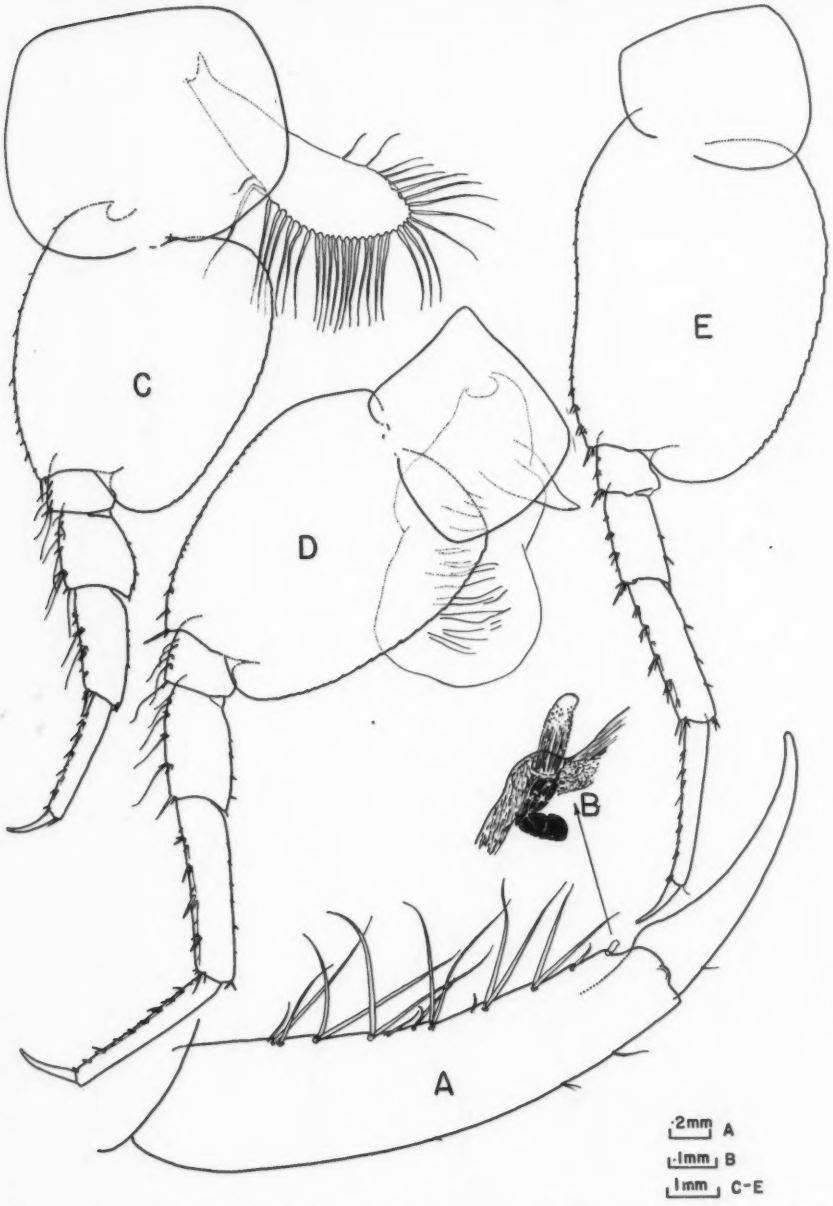

FIG. 3. *Anonyx nugax* (Phipps). Mature female, 41 mm, St. Lawrence Estuary, D 36. A, peraeopod 3; B, spur of peraeopod 3; C, peraeopod 5; D, peraeopod 6; E, peraeopod 7.

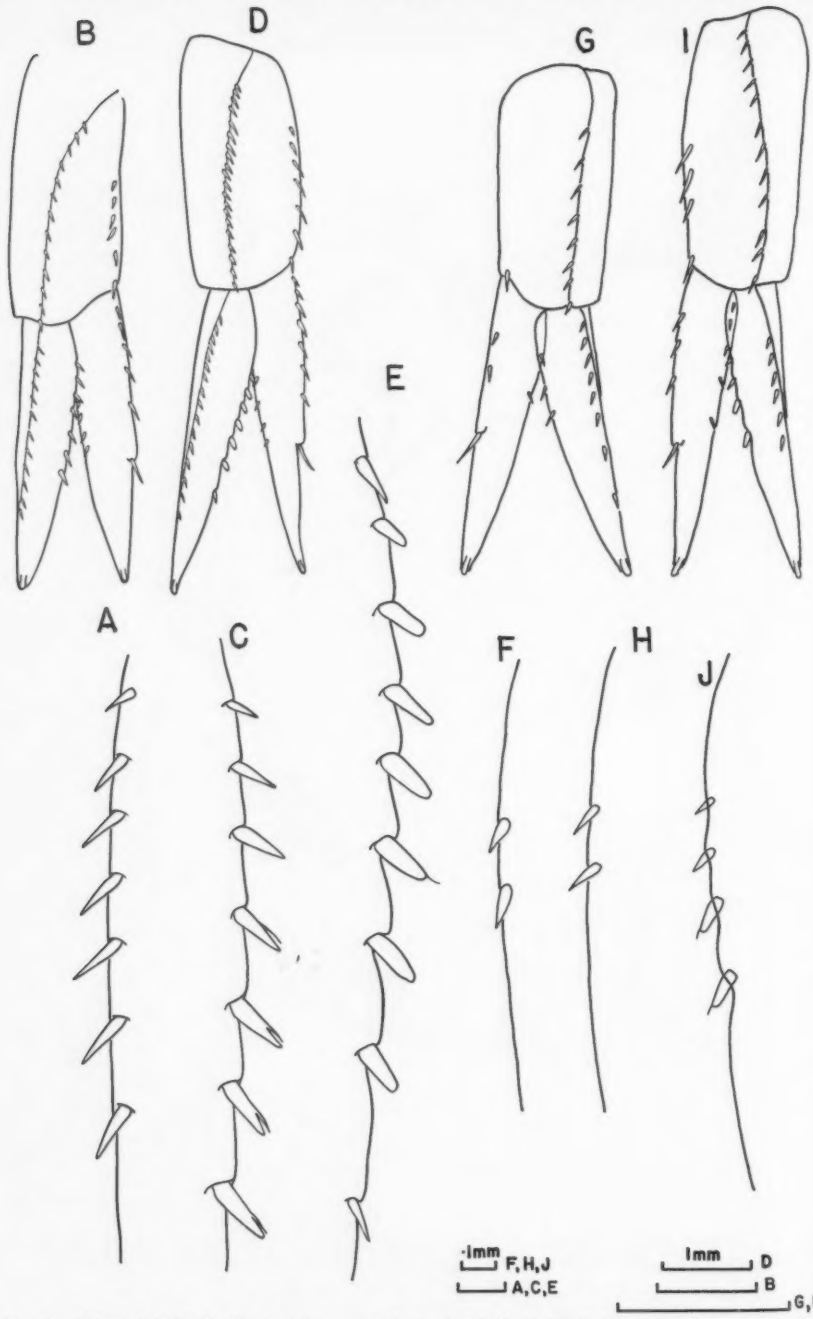

FIG. 4. Uropod 2. B, D, G, I, entire appendage; A, C, E, F, H, J, inner edge of outer ramus. A–E, *Anonyx nugax* (Phipps). A, mature female, 38 mm, Turton Bay, Foxe Basin; B, C, immature male, 32 mm, Tern Island, Foxe Basin; D, E, mature male, 39 mm, Turton Bay, Foxe Basin. F–J, *Anonyx sarsi* n.sp. F, mature female, 26 mm, Pt. Burwell, Ungava Bay; G, H, immature male, 22 mm, Pt. Burwell, Ungava Bay; I, J, mature male, 22 mm, Gulf of St. Lawrence.

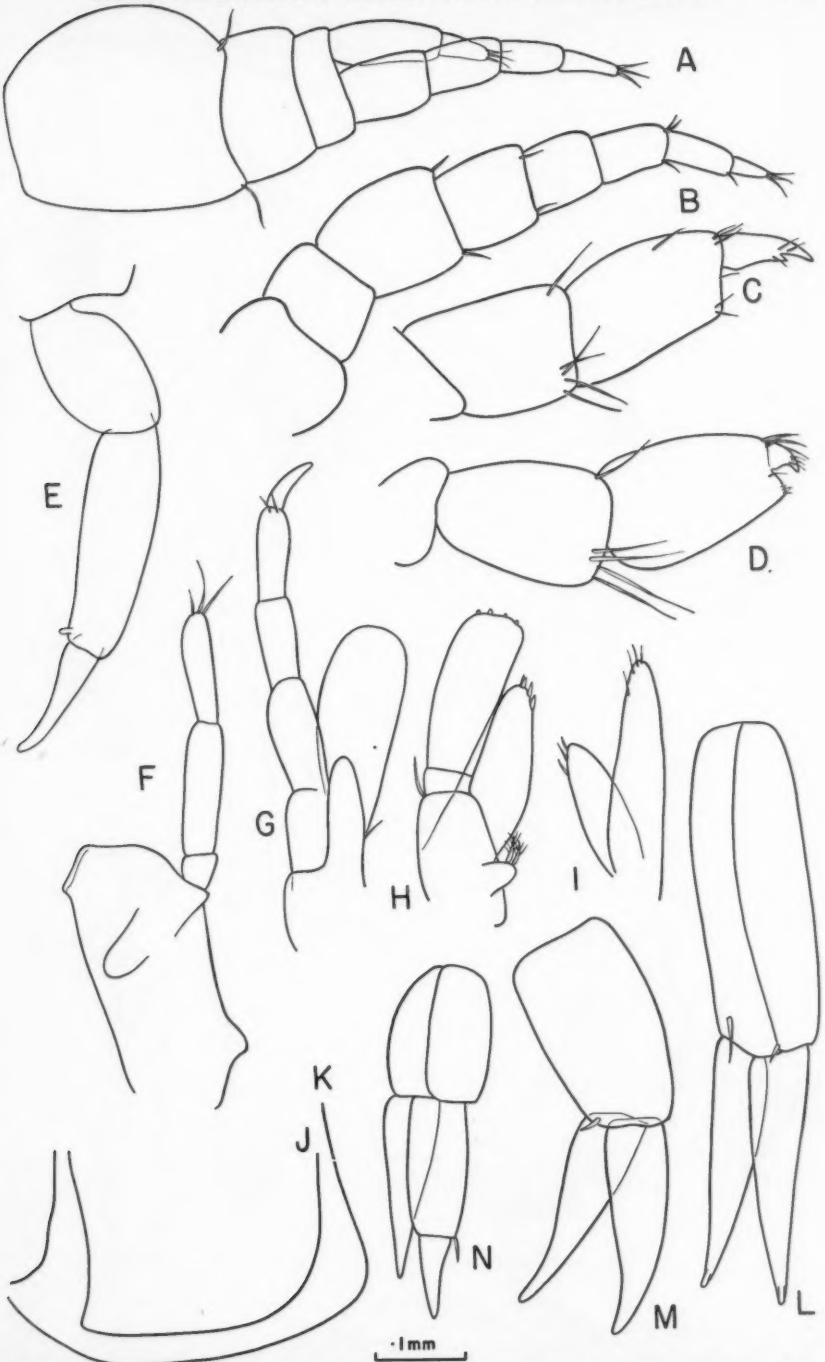

FIG. 5. *Anonyx nugax* (Phipps). Immature, 3 mm, from brood pouch of 36-mm female from West Greenland (Olrik, 1866). A, antenna 1; B, antenna 2; C, peraeopod 1; D, peraeopod 2; E, peraeopod 3; F, right mandible; G, maxilliped; H, maxilla 2; I, maxilla 1; J, lateral plate of second metasome segment; K, lateral plate of third metasome segment; L, uropod 1; M, uropod 2; N, uropod 3.

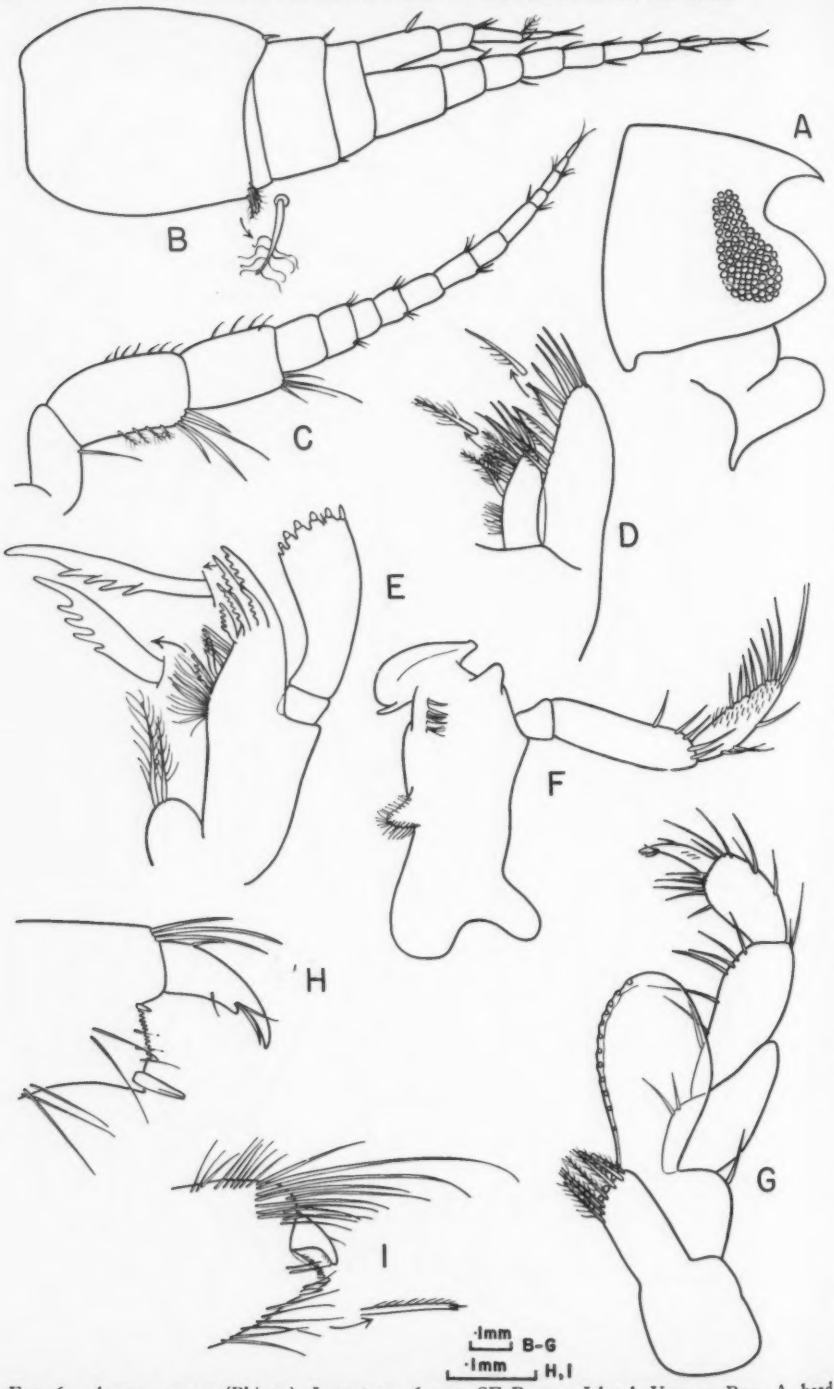

FIG. 6. *Anonyx nugax* (Phipps). Immature, 6 mm, SE Beacon Island, Ungava Bay. A, head and upper lip; B, antenna 1; C, antenna 2; D, maxilla 2; E, maxilla 1; F, right mandible; G, maxilliped; H, peraeopod 1; I, peraeopod 2.

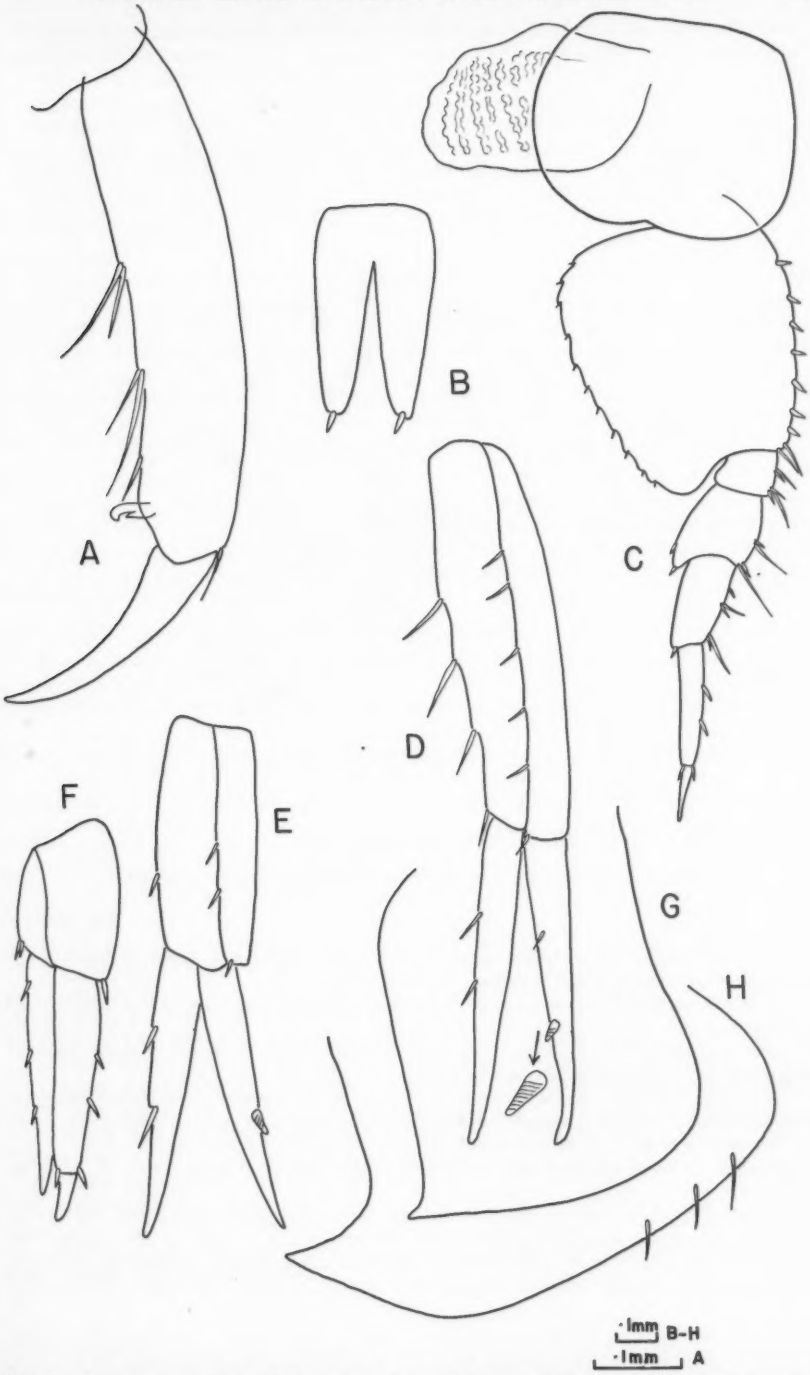

FIG. 7. *Anonyx nugax* (Phipps). Immature, 6 mm, SE Beacon Island, Ungava Bay. A, peraeopod 3; B, telson; C, peraeopod 5; D, uropod 1; E, uropod 2; F, uropod 3; G, lateral plate of second metasome segment; H, lateral plate of third metasome segment.

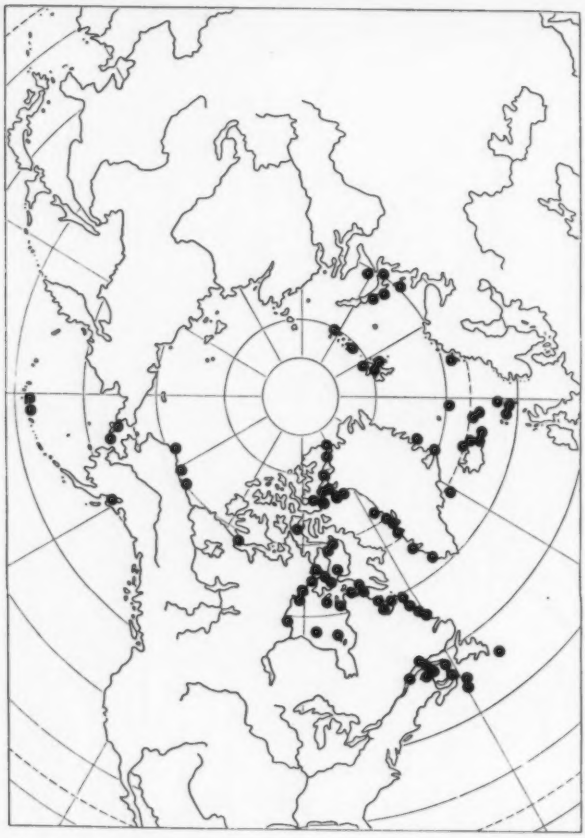

FIG. 8. Distribution of *Anonyx nugax* (Phipps) based on examined material.

Branchial vesicles.—On peraeppods 2–6, pleated into transverse ridges; on peraeopod 7, unpleated; on peraeopods 5 and 6, with an accessory lobe.

Metasome segment 1.—Anterior edge of the lateral plate setose, produced anteriorly at the lower corner.

Metasome segment 2.—Lateral plate, anterior and ventral edges setose, lower posterior corner produced into a prominent acute tooth.

Metasome segment 3.—Not carinate dorsally. Lateral plate setose ventrally and anteriorly, posterior projection short and extending into a short acute tip with a concave lower edge.

Urosome segment 1.—Slightly carinate dorsally and projecting posteriorly.

Uropod 1.—Rami almost equal, with medium-sized marginal spines, none of which are ridged.

Uropod 2 (*Fig. 4*).—Rami almost equal. Inner ramus slightly constricted just beyond the middle and bearing a medium-sized spine at the level of the constriction. This spine is one and a half to two times the length of the short proximal spines, and one-quarter to one-fifth of the distance from it to the end of the ramus. Outer edge of the inner ramus with a row of small

spines; outer ramus bearing small spines on its outer edge and, on its inner edge, fairly short spines, the distal ones not longer than the proximal ones and not extending into the distal third of the ramus; the larger spines have an accessory hair but none are ridged.

Uropod 3.—Outer ramus broad, tapering from the anterior third, with spines on the inner and outer edges and the ventral surface, plumose setae on the inner edge, and a short second segment (one-tenth of the proximal). Inner ramus broad, tapering from the middle, shorter than the outer, with spines on the inner and outer edges and plumose setae on the inner edge.

Telson.—Deeply cleft, with three to four spines and a pair of setae on the dorsal surface and a single spine and short hair inserted in the distal notch of each lobe.

Mature Male

The mature male is similar to the female except that the antennae are longer and composed of more and longer segments bearing calceoli. The inner edge of the outer ramus of uropod 2 is serrated, with a blunt spine inserted in each notch. These blunt spines appear to be formed in the last moult by the loss from each spine of the portion distal to the accessory hair seta. The eye may also be proportionately larger and more expanded antero-ventrally, but this is sometimes difficult to distinguish in preserved material. Mature individuals with still more enlarged eyes, presumably for pelagic swarming, have been found in the collections (e.g. in three samples, G72, D201, D202, from south of Anticosti Island, Gulf of St. Lawrence, in June and August).

Young

Few ovigerous females were found in any of the collections that were studied. Early stage embryos of *A. nugax* are oval in shape and generally range in size when preserved in alcohol from 1.3 × 1.1 mm to 1.7 × 1.4 mm (Table I). The specimen collected by the *Knight Errant* in the Faeroe Channel contained unusually large embryos in its brood pouch. The young hatch at a size of 2.9–3.2 mm (Table I).

Description of Newly Hatched Young (3.0 mm) (Fig. 5)

Specimens of this size lack most of the distinctive features of the species and would in fact be difficult to refer to the genus *Anonyx*. The first antenna is as long as the second; the first segment of the peduncle is large and bulbous, with only a few simple setae; the flagellum has

Table I. Sizes of early embryos and hatched young from the brood pouch of ovigerous females of *Anonyx nugax*.[a]

Locality	Size of female	No. measured	Length (*mm*) Mean	Length (*mm*) Range	Diam (*mm*) Mean	Diam (*mm*) Range
Early embryos						
Kara Sea, Norman collections	41	5	1.7	1.6–1.8	1.4	1.5–1.4
Faeroe Channel, "Knight Errant" St. 8	33	5	2.3	1.7–2.5	1.9	1.6–2.0
Brede Bugt, W Greenland	31	6	1.3	1.3–1.5	1.1	1.0–1.3
W Greenland, Godthaab Exp. St. 107	42	5	1.5	1.4–1.5	1.0	1.0–1.1
W Greenland, Jacobshavn	32	5	1.5	1.4–1.5	1.0	1.0–1.1
S Anticosti Is., Gulf St. Lawrence (Sta. Biol. Mar., D201)	35	10	1.27	1.25–1.4	1.0	1.0
Hatched young						
Spitzbergen Lyneum Hbr.	39	5	3.0	2.9–3.0		
W Greenland, Olrik 1866	36	5	3.1	3.0–3.2		

[a]All measurements of this and other species are of preserved material and consequently must be accepted with reservations.

four segments and is equal in length to the peduncle. Antenna 2 is short with a few simple setae and a four-segmented flagellum. The mandible lacks a spine row and teeth on the cutting edge; the molar is small and conical; the palp is well developed but with only a few setae on the apex of the third segment. The inner lobe of the first maxilla has two long plumose setae; the outer lobe is elongated and rounded at the tip and bears only a few short simple spines; the palp is elongated, with the second segment expanded and bearing a few short teeth at the apex. Both lobes of the second maxilla are elongated and bear only a few short setae; the inner is more than half the length of the outer. The inner lobe of the maxilliped is rounded distally with only a single simple seta on the inner margin; the outer lobe is broadly expanded; the palp is narrow and elongated. The first peraeopod has its coxal plate expanded anteriorly, its sixth segment equal to the fifth, a broad, perpendicular palm defined by two small setae; the dactyl is slightly longer than the palm and bears an accessory tooth and a few setae on the inner margin. The sixth segment of peraeopod 2 is equal in length to segment 5; the palm is relatively long and produced only slightly under the proportionately large dactyl. Segment 6 of peraeopods 3 and 4 has a blunt simple spine at the posterior lower corner. The lateral plate of the second metasome segment is concave and produced slightly at the lower posterior angle but is not distinctly toothed. The posterior projection of the lateral plate of the third metasome segment is small. The uropods have only a few simple setae; the inner ramus of uropod 2 is not constricted; the distal segment of the third uropod is almost three-quarters of the length of the proximal segment.

Description of 6-mm Specimens (Fig. 6–7).

The smallest specimens (6 mm) identified in collections differ considerably from the newly hatched young and are readily identified as *Anonyx*. However, they differ in many respects from the larger specimens and it is difficult to identify them as this species.

The eye is less expanded ventrally than in the adult, has a straight posterior margin, is more reddish in colour, but does occupy most of the interantennal lobe. The upper lip is more rounded and, although generally small, extends proportionately farther in front of the epistome. The first antenna is relatively long, with a few setae; the first segment of the peduncle is longer than it is deep and a cluster of feathery setae occurs at its lower anterior corner. Antenna 2 is similar to that of the adult but with fewer setae and segments in the flagellum. The right mandible is also similar to that of the adult, except for the third segment of the palp which is shorter, rounded distally, and more obviously hairy. (The marginal setae lack the plumose character of those of the adult.) The spines on the outer lobe of the first maxilla have from two to five accessory teeth; the second segment of the palp is distally expanded but has only five socketed teeth on stalks and a single unstalked tooth. The second maxilla and the maxilliped are generally similar to those of the adult. The dactyl of peraeopod 1 has a prominent accessory tooth on the inner margin. The sixth segment of peraeopod 2 is three-quarters of the length of segment 5; the palm is straight and noticeably produced under the moderately large finger; the latter bears short hair but no teeth on its inner margin. The inner setae of the pairs on the hind margin of segment 6 of peraeopods 3 and 4 are short, often only one-half to three-quarters of the length of the outer; the blunt spine is strongly hooked and has a large accessory tooth. The posterior margin of segment 2 on peraeopod 7 has a few conspicuous well-projecting teeth. The pleating of the branchial vesicles is weakly developed or absent. The lateral plate of the second metasome segment has a straight posterior margin and is produced at the lower corner into a conspicuous tooth. The posterior projection of the lateral plate of the third metasome segment is evenly rounded ventrally, without any concavity. The distal spine on the outer margin of the outer ramus of uropod 1 is stout and ridged. The inner ramus of uropod 2 is constricted just beyond the middle and the spine therein is relatively long (one-third of the distance from it to the end of the ramus); the inner edge of the outer ramus is without spines (they appear at a size of 9–10 mm); the distal spine on the outer edge of the outer ramus is stout and ridged. The rami of uropod 3 are narrow, without setae; the second segment of the outer ramus is one-quarter of the length of the proximal segment. The telson is elongated and cleft to three-quarters of its length.

TYPE-SPECIMENS

Cancer nugax Phipps, 1774. Type-locality: West of Moffen Island Spitzbergen (about 80°10′N, 12°30′E), July 25, 1773, trawl, probable depth between 2 and 13 fath (3.7–24 m), the depth range of soundings recorded in Phipps' log book for the day. The holotype has never been mentioned by any author, to our knowledge, and we have not found it in the British Museum.

Anonyx lagena, Krøyer, 1838a (holotype). One male with copulatory papillae, about 35 mm (length given by Krøyer, 1846: 14 lines). "i Hager, Umanak, Grönland. Fleischer. TYPE." Umanak: 70°42′N, 51°59′W. Universitetets Zoologiske Museum, Copenhagen. The specimen is broken into four pieces, the antennal flagella are lost, the head is almost completely empty, and much of the armature of spines and setae has been worn away, including that of segment 6 on the third and fourth peraeopods. It is not advisable, therefore, to use this specimen as a neotype.

Anonyx appendiculosa Krøyer, 1838a (holotype; paratype of *A. lagena*). One male with calceoli on the antennae, 32 mm (length given by Krøyer, 1846: 12 lines). Same data as *A. lagena*. Univ. Zool. Museum, Copenhagen. The specimen is very well preserved.

Anonyx lagena Krøyer (or? *Anonyx ampulla* Krøyer, 1846). One female with developing nonsetiferous oostegites, 36 mm (length given by Krøyer, 1846: 16 or 17 lines). One label: "TYPER Spitsbergen. Krs' Originalex. Samlet Opstillet, og testernt af Kr." Other label: "Spitsbergen. Krøyer leg." Univ. Zool. Museum, Copenhagen. This specimen is in a very good state of preservation. (The other specimen found with this "type" was smaller (28 mm) and we identified it as *Anonyx laticoxae* Gurjanova, 1962.)

Anonyx ampulloides Bate, 1862 (holotype). One immature individual about 10 mm Japan. Collected by William Stimpsom. British Museum (Natural History), London, Cat. No. 68–107.

Lysiannassa Fisheri Lockington, 1877. One specimen, 1.38 inches long, "including stylets" (i.e. about 32 mm to the tip of the telson). West coast of Alaska, W. J. Fisher. The specimen was dried already at the time of its description. Holmes (1904) erroneously gives the northern coast of Alaska as the type-locality.

Anonyx kukenthali Vosseler, 1889. No single specimen or exact locality, other than Spitsbergen, is given with original description. Collected by Willy Kükenthal. Size of largest: 22 mm. A collection of specimens in samples collected at Spitsbergen by W. Kükenthal, and labelled *A. nugax*, probably represent the syntypes. Zoologiskes Museum, Hamburg.

Lakota chelata Chevreux, 1926 (holotype). One immature individual, 4.5 mm. Off the Lofoten Islands, western Norway (69°18′15″N, 14°29′15″E), depth 1095 m, July 20–21, 1898, "Princesse Alice," sta. 945 (or 145?). Muséum National d'Histoire Naturelle, Paris, Cat. No. 1898. There are only microscopic slides with badly preserved preparations. No oostegites are to be seen, and it is difficult to understand how Chevreux could identify it as a female at such a small size.

REMARKS

Phipps' type-specimen has not been found, but since the form described above is evidently the most abundant and largest species of *Anonyx* at the type-locality (Moffen Island, Spitsbergen), it is probable that it is that which Phipps described and named *Cancer nugax*. Krøyer's two type-specimens of *Lysianassa* (*Anonyx*) *lagena* and *Lysianassa* (*Anonyx*) *appendiculosa* from Umanak, West Greenland, which Hansen (1887) had not found, were discovered in the Copenhagen Museum and kindly sent to us by Dr Torben Wolff. They both proved to be *A. nugax*, as described here, although both are males, contrary to the impression given by Krøyer's (1838a, 1842) descriptions. Although other specimens identified by Krøyer were actually *A. lilljeborgi* (from Norway), a vial containing two complete specimens labelled "*Anonyx lagena* Krøyer, TYPER, Krs' Originalex., Spitsbergen," from the Copenhagen Museum, upon examination yielded one *A. nugax*, a 36-mm immature female,

and one 28-mm mature male of *A. laticoxae*. Since Krøyer's elaborate description and synonymy (1846) and his accurate figure (1846?) were the first to fix accurately the identity of *Anonyx nugax*, whatever the name (*A. ampulla*) he then retained for it, and since by that time he had secured specimens (which he mentions) from Spitsbergen (two of 16 and 17 lines) and from the Trondheim Fjord, in addition to his Greenland specimens (two of 12 and 14 lines), the two Spitsbergen types must have been labelled as such because they had served as models to Krøyer (1846, 1846?). Therefore, they retain some importance in spite of the discovery of the Greenland types. Four clues, however, lead one to suspect that they may have been singled out as types after Krøyer's death, and may not have the most secure authenticity: (*a*) the wording on the label refers to Krøyer as a third person; (*b*) the name *Anonyx lagena* appears on that label, rather than *A. ampulla*; (*c*) the Spitsbergen specimens are not both larger than the Greenland types, as Krøyer states, but one (the true *nugax*) is larger, and the other (*laticoxae*) a little smaller; (*d*) one of the two "types" is *A. laticoxae*, a species of which we have but a single other record (Franz Joseph Land) from the northeastern Atlantic, but which occurs more commonly in the northwestern Atlantic, including western Greenland. Whatever the status of the Spitsbergen "types," one may observe that the constricted inner ramus, with long spine, of uropod 2 illustrated by Krøyer (1846?) for *ampulla* excludes from consideration, as type for that name, the smaller of the two specimens, which we have identified as *A. laticoxae*, and leaves only that which we refer to as *A. nugax*. This is fortunately in agreement with our identification of the two Greenland types, so that the identity and early synonymy of *A. nugax* are not in danger of being contested.

The changes in morphology with size and age, which have not been described previously, have led some investigators into describing the young as separate species. Thus, Bates' type-specimen of *Anonyx ampulloides* is small, immature, broken into two pieces, and thus difficult to identify with certainty without dissection, but appears to be a young *A. nugax*. Chevreux's type-specimen of *Lakota chelata* was also examined and found to be a small individual of *A. nugax*.

It seems probable that Vosseler's *A. kukenthali*, which Stebbing (1906) places in the synonymy of *nugax*, also belonged to this species. Although the holotype cannot be identified as such, Vosseler's paper does not record the common Spitsbergen *A. nugax* in the small collection he had for study. Yet the Hamburg Zoologisches Museum has a collection of specimens collected by Kükenthal at Spitsbergen, which are now labelled *A. nugax*, and which proved to contain six *A. nugax*, one *A. sarsi*, one *Socarnes bidenticulata*, and one *Weyprechtia pinguis*. Four *nugax* specimens are larger than the maximum of 22 mm given by Vosseler for *kukenthali*. Lockington's (1877) type-specimen of *Lysianassa fisheri* being lost, Holmes' (1904) opinion that it is synonymous with *A. nugax* cannot be confirmed: it may have belonged to other large Pacific species now known from the area.

It is apparent from our descriptions that *A. nugax* undergoes quite pronounced changes in its morphology from the time it hatches until it reaches its final size. It is worth emphasizing that the young stages bear a strong resemblance to the adults of small related species and even more to their young.

Variation

Our examination of specimens from the region between the Kara Sea to Alaska (including the type-locality of Spitsbergen) has failed to reveal any appreciable geographic variation, except as noted below. Specimens from this whole area are readily identified as this species and agree essentially with the description presented above.

However, Gurjanova (1962) has claimed that differences exist between specimens from the Kara and Siberian seas and those of the Barents and Norwegian seas, and considered specimens from the former area as the typical form of the species. The Barents Sea specimens described by Gurjanova (1962) resemble our specimens closely except for their smaller eyes. This is a characteristic which may vary with preservation, sex, and size, and cannot be regarded as critical. On the other hand, the specimens she described from the Siberian seas differ from ours in several respects (Table II), not the least of which is their huge size (65 mm for males, 62 mm for females, from the Kara Sea) at maturity.

Table II. Comparison of *Anonyx nugax* from Siberian seas (Gurjanova, 1962) with those of the area from the Kara Sea westward to Alaska.

	Siberian seas	Kara Sea to Alaska
Eye	Small, height equal to one-half the height of the head, not occupying the interantennal lobe	Large, equal to two-thirds to three-quarters the height of the head, occupying most of the interantennal lobe
Peduncle of antenna 2	Distal segment equal in width to, and shorter than, the penultimate	Distal segment narrower than, and equal in length to, the penultimate
Palm of peraeopod 1	Concave	Straight
Peraeopods 3 and 4	Long seta in front of the blunt spine	Without the long seta in front of the blunt spine
Lateral plate of metasome 3	Without ventral setae	With ventral setae
Peraeopod 5	Second segment narrowed distally, fourth segment narrower than long	Second segment not narrowed distally, fourth segment almost as broad as long
Maximum size at maturity	65 mm	44 mm

It is apparent that with the exception of size, the armature on peraeopods 3 and 4, and the lateral plate of the third metasome segment, these are minor characters that may be varied to some extent by mounting the parts for examination, and are therefore subject to differences in interpretation. Even if they are real variations they cannot be regarded as characters typical of *A. nugax* because they are not shared by specimens from Spitsbergen, the type-locality. It is possible, therefore, that the Siberian form of Gurjanova represents a subspecies or even a species distinct from *A. nugax*.

The size at maturity of *A. nugax* generally increases from south to north (Table III). There are some regional differences in the morphology of mature specimens which appear to be related to the size of the specimens rather than to geographic areas. The larger individuals have a greater development of spines and setae and somewhat different proportions and shapes. Thus the number of proximal spines on the inner edge of the inner ramus of uropod 2 is usually 5, but in large specimens it is often 6, and in the very large specimens from the Kara Sea it may reach 9 or 10.

TABLE III. Size (mm) at maturity of *Anonyx nugax* in different areas.

	Male		Female	
	Maximum size of immature individuals	Size-range of mature individuals	Maximum size of immature individuals	Size-range of mature individuals
Kara Sea	47	46	42	41
Novaya Zemlya	–	37	–	–
Spitzbergen	–	–	41	39
Norwegian Sea	37	38–45	–	–
Faeroe Channel	–	–	30	33
Northwest Greenland and Ellesmere Island	35	35–37	38	–
West Greenland	39	31	43	31–42
Foxe Basin	33	34–39	41	38–40
Hudson Strait	33	43	38	–
St. Lawrence Estuary (deep water)	40	32–40	35	41
Gulf of St. Lawrence (shallow and deep water)	28	27–33	29	35

DISTRIBUTION

Anonyx nugax probably has a circumpolar distribution since it is recorded here from the Kara Sea west to Bering Strait and was reported by Gurjanova (1962) from the Siberian seas. It has essentially a northern distribution and in the northwestern Atlantic is found only as far south as the Scotian Shelf. In the Gulf of St. Lawrence it seems to be typical of the deeper

waters of the Laurentian Channel, and to be scarcer in the intermediate cold-water layer where it is replaced by *A. pacificus* as the dominant form; however, in the northwest of the Gulf and perhaps in the St. Lawrence Estuary, where upwelling of deep water occurs, it seems to be abundant in shallow water, at least at breeding time. From Labrador northward, it is by far the most common species of the genus and occurs in shallow water almost to the shoreline as well as in the deeper offshore waters. The distribution appears to be similar in the eastern Atlantic and the northern Pacific where the southern records are from fairly deep water.

Anonyx pacificus Gurjanova, 1962

SYNONYMY

Anonyx nugax pacificus Gurjanova, 1962, p. 219, fig. 68–A–B(?), 69A–B.

DIAGNOSIS OF MATURE FEMALE

Medium-size, upper lip with a ventral rounded angle and moderately produced in front of the epistome, segment 6 of peraeopod 1 narrowed slightly distally, dactyl of peraeopod 1 without an accessory tooth, dactyl of peraeopod 2 small, posterior edge of segment 6 of peraeopods 3 and 4 with a row of paired long setae and a few unpaired slender spines, segment 2 of peraeopod 7 prominently and coarsely serrated on distal hind edge, shorter than rest of the limb, inner ramus of uropod 2 constricted well beyond the middle and bearing a medium-size spine at the constriction, second metasome lateral plate with a distinct tooth on the postero-ventral corner, posterior projection of the third metasome lateral plate produced into an acute ventrally concave point.

DESCRIPTION OF MATURE FEMALE

This species matures at a size of 27–34 mm.

Head.—Shorter than the combined length of the first two segments of the mesosome. Interantennal lobe right-angled and less rounded than in *A. nugax*, lower margin straight. Eye large, expanded ventrally and occupying most of the interantennal lobe, posterior margin concave, red-brown to black in colour.

Antenna 1.—Peduncle large, shorter than the head, segment 1 longer than it is high, dorsal profile nearly straight. Flagellum short, first three segments and third segment of the peduncle with single short rods (aesthetascs?) on their medial surface.

Antenna 2.—Fourth and fifth segments of the peduncle with dorsal rows of short setae and ventral rows of feathery setae. Fourth segment with an outer ventral row of long setae and fifth segment with four groups of long setae on the ventral edge. Flagellum short, with long ventral setae.

Upper lip.—Extending well in front of the epistome as a ventrally angular rounded lobe.

Right mandible.—With a single large tooth on the cutting edge. Three spine-teeth and four or five hairy setules in the spine row. Palp strong, second segment cylindrical and equal in length to the third, which is finely hairy on the anterior surface; posterior margin with coarse setae, pectinate on their medial surface.

Left mandible.—With two teeth on the cutting edge.

Maxilla 1.—Outer lobe bearing six broad short spines and five longer spines each with one to two accessory teeth. Palp broadly expanded and bearing nine conical socketed teeth on tall widely spaced stalks, and one small unsocketed tooth on the inner corner.

Peraeopod 1.—Coxal plate setose medially, expanded anteriorly and rounded, maximal width shorter than the height below the antero-proximal corner. Sixth segment equal in length to the fifth, narrowed only slightly distally, palm perpendicular, defined by two stout spines with accessory hair. Dactyl not much longer than the palm, without an accessory tooth.

Peraeopod 2.—Sixth segment half as long as fifth, covered distally and ventrally by long setae with a forked tip and a pectinate medial margin; palm concave, produced slightly under the small finger which is setose and distally denticulate on the inner margin.

Peraeopods 3 and 4.—Posterior edge of the sixth segment with a row of pairs of long setae and a few elongated spines, the latter not paired with the long setae; blunt spine at the posterior margin of segment 6 apically narrowed, only slightly hooked and lacking an accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with more than 20 serrations, those of the distal half distinctly more crowded and prominent than the proximal ones; maximal length of the segment distinctly shorter than the rest of the limb.

Branchial vesicles.—Those of peraeopods 2–6 pleated into transverse ridges; those of peraeopod 7 unpleated; those of peraeopods 5 and 6 with a small accessory lobe.

Metasome segment 1.—Anterior edge of the lateral plate setose and produced anteriorly at the lower corner.

Metasome segment 2.—Anterior and ventral edges of the lateral plate setose, lower posterior corner produced into a prominent acute tooth.

Metasome segment 3.—Not carinate dorsally. Lateral plate setose ventrally and anteriorly, produced posteriorly into a ventrally rounded projection which extends posteriorly into an acute tip with a concave lower posterior edge. (The projection is noticeably more acutely produced and the ventral margin more concave than in *A. nugax*.)

Urosome segment 1.—Slightly carinate dorsally and projecting posteriorly.

Uropod 1.—Rami almost equal, with long spines (none of which are ridged) on their inner margin.

Uropod 2.—Rami almost equal in length. Inner ramus slightly constricted well beyond the middle (two-fifths to one-third of the distance from the end) and with a medium-size spine at the level of the constriction. This spine is only slightly longer (one and one-quarter to one and a half times) than the medium-size proximal spines and its length is one-third to one-quarter of the distance from it to the end of the ramus. Outer edge of the inner ramus bearing a row of medium-size spines. Outer ramus with medium-size spines on the inner edge and small spines on the outer edge, the former spines increasing in length distally and occurring in the distal third of the ramus; none of the spines are ridged but they may bear an accessory hair.

Uropod 3.—Outer ramus broad, tapering from the anterior third, bearing spines on the inner and outer edges and on the ventral surface, plumose setae on the inner margin; second segment short (one-tenth of the length of the proximal segment). Inner ramus broad, tapering from the anterior third, shorter than the outer, with spines on the inner and outer margins and plumose setae on the inner edge.

Telson.—Deeply cleft, with three spines and a pair of setae on the dorsal surface and a single spine and short hair inserted in a notch at the apex of each lobe.

Mature Male

The antennae are longer than those of the female and they are composed of more and longer segments with calceoli. The eye is also larger and occupies almost all of the interantennal lobe. The uropods have more spines and setae; the inner margin of the outer ramus of uropod 2 is not serrated and bears medium-size distal spines and a few short blunt proximal spines.

Young

No ovigerous females were obtained in any of the collections and the smallest specimens that could be identified with certainty as this species were 5–6 mm long. These are identical in most respects with similar-size *A. nugax* and only the structure of uropod 2 will serve to distinguish them. In *A. pacificus*, firstly, the inner ramus is constricted well beyond the middle (almost one-third of the distance from the end) and the spine at the constriction is long (at least three-quarters of the distance to the end of the ramus); secondly, in specimens longer than 9 mm, the outer ramus often bears, on the distal third of its inner edge, a spine which is usually as long as or longer than the width of the ramus at the level of the insertion of the spine. The spine, which is lacking in *A. nugax*, may be difficult to see since it is closely pressed along the edge of the ramus. Also, in specimens of about 10 mm, there may be a shorter spine, or a shorter spine on one uropod and

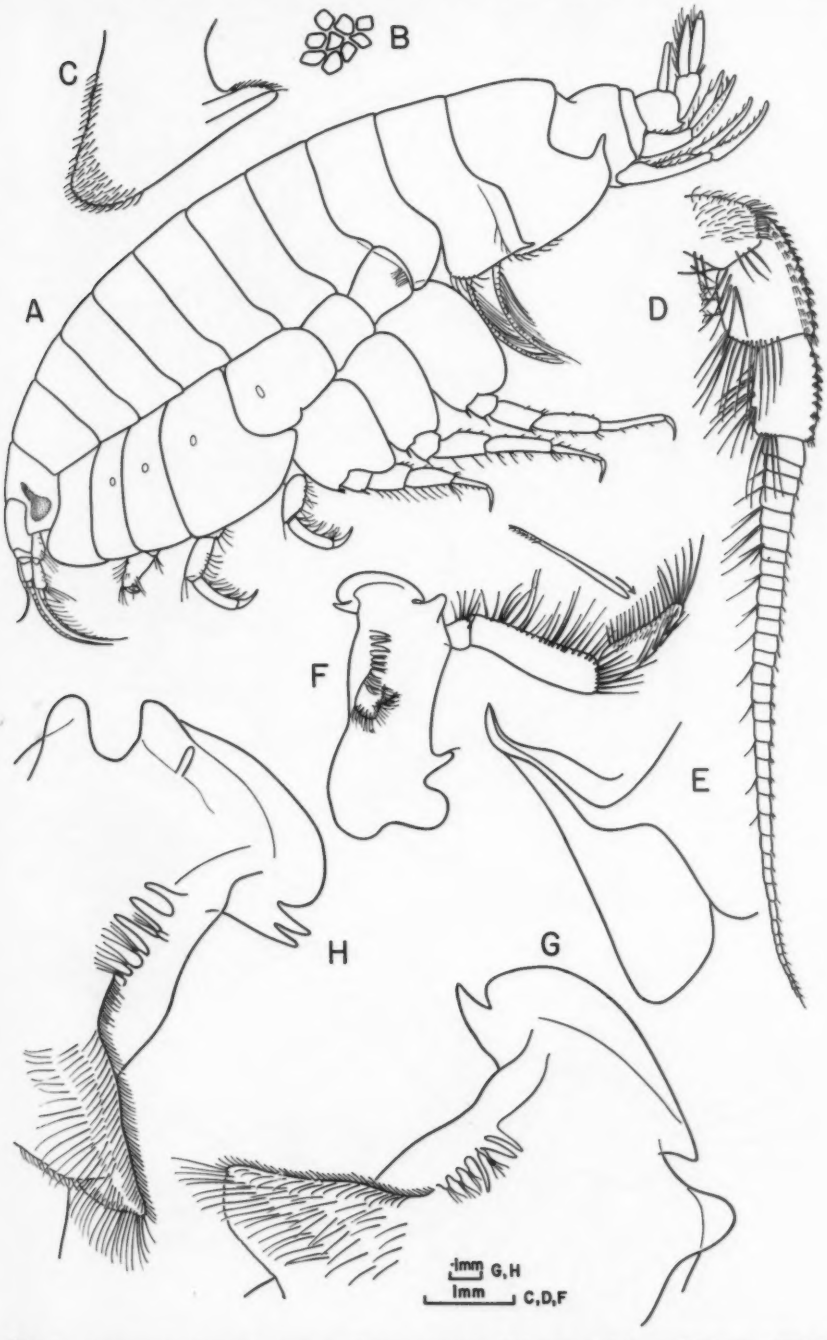

FIG. 9. *Anonyx pacificus* Gurjanova. Mature female, 32.5 mm, Schooner Harbour, Hudson Strait. A, whole animal; B, sculpturing; C, lower lip; D, antenna 2; E, upper lip; F, G, right mandible; H, left mandible.

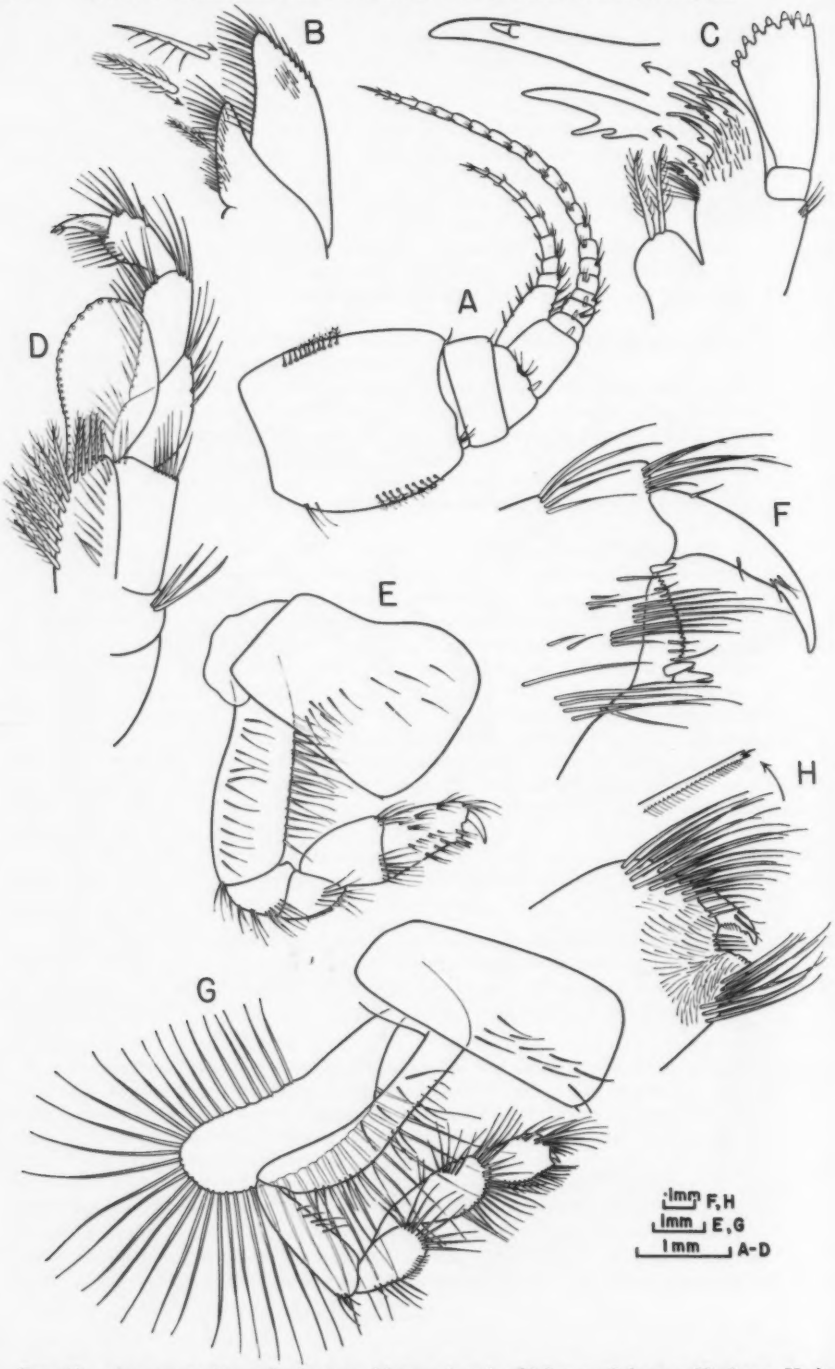

FIG. 10. *Anonyx pacificus* Gurjanova. Mature female, 32.5 mm, Schooner Harbour, Hudson Strait. A, antenna 1; B, maxilla 2; C, maxilla 1; D, maxilliped; E, F, peraeopod 1; G, H, peraeopod 2.

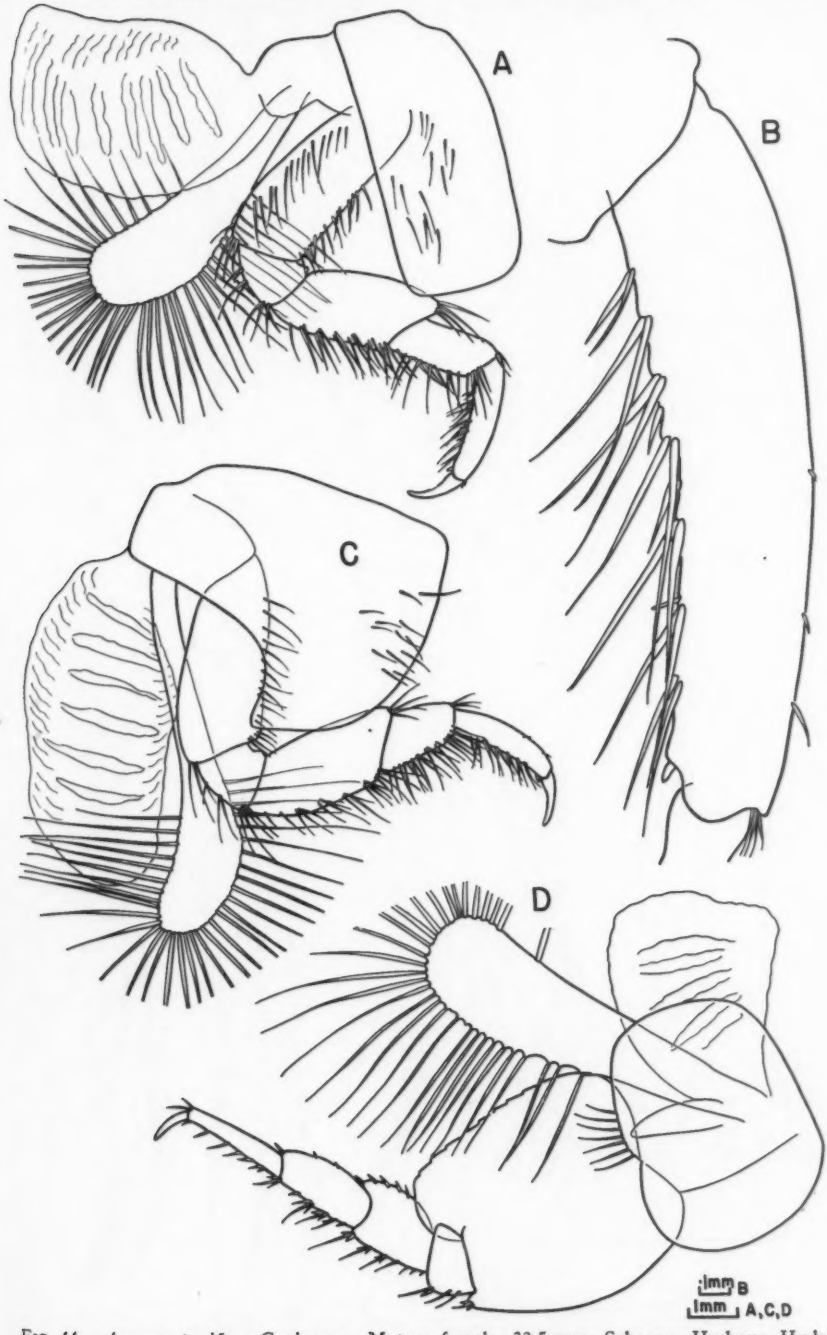

FIG. 11. *Anonyx pacificus* Gurjanova. Mature female, 32.5 mm, Schooner Harbour, Hudson Strait. A, B, peraeopod 3; C, peraeopod 4; D, peraeopod 5.

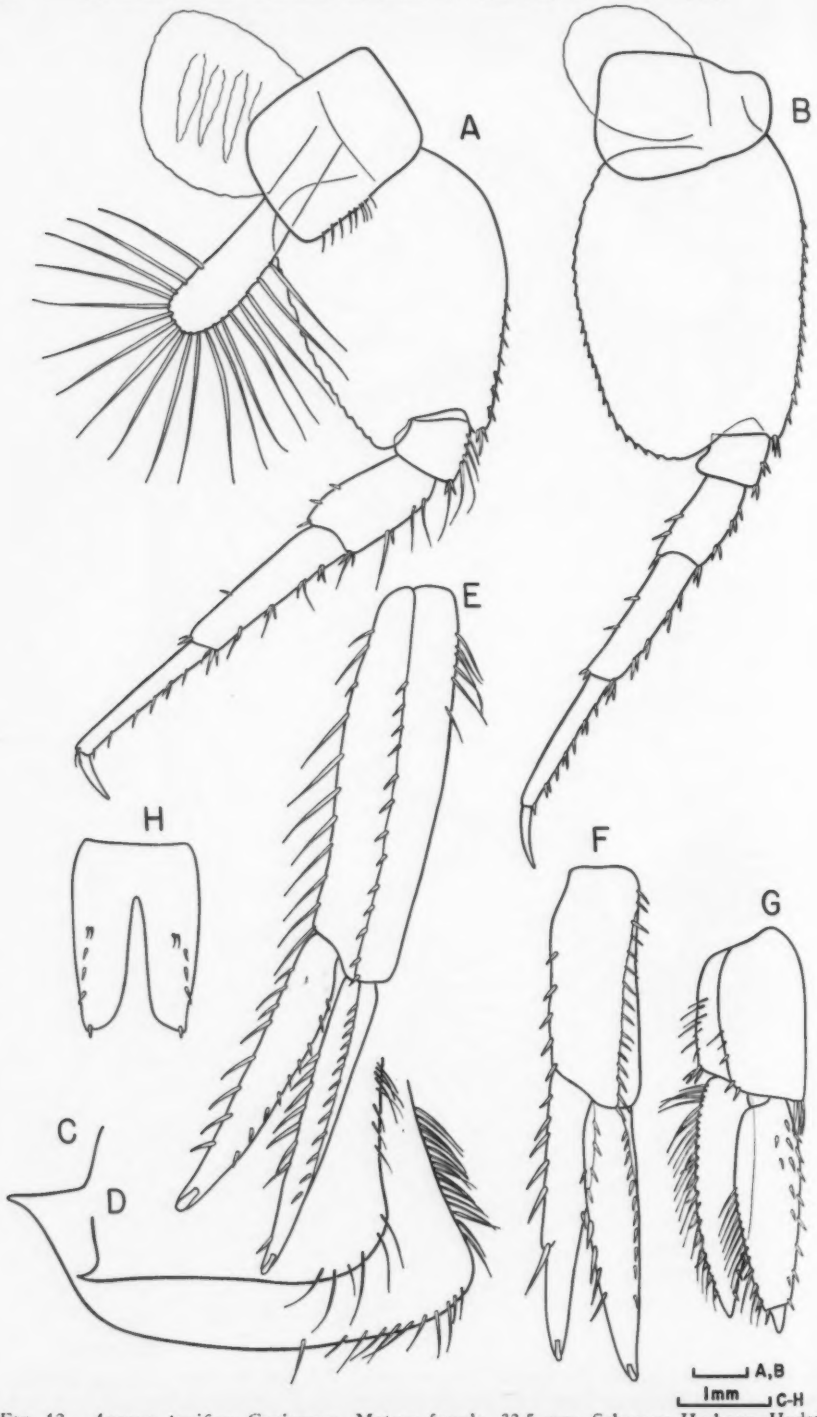

FIG. 12. *Anonyx pacificus* Gurjanova. Mature female, 32.5 mm, Schooner Harbour, Hudson Strait. A, peraeopod 6; B, peraeopod 7; C, lateral plate of third metasome segment; D, lateral plate of second metasome segment; E, uropod 1; F, uropod 2; G, uropod 3; H, telson.

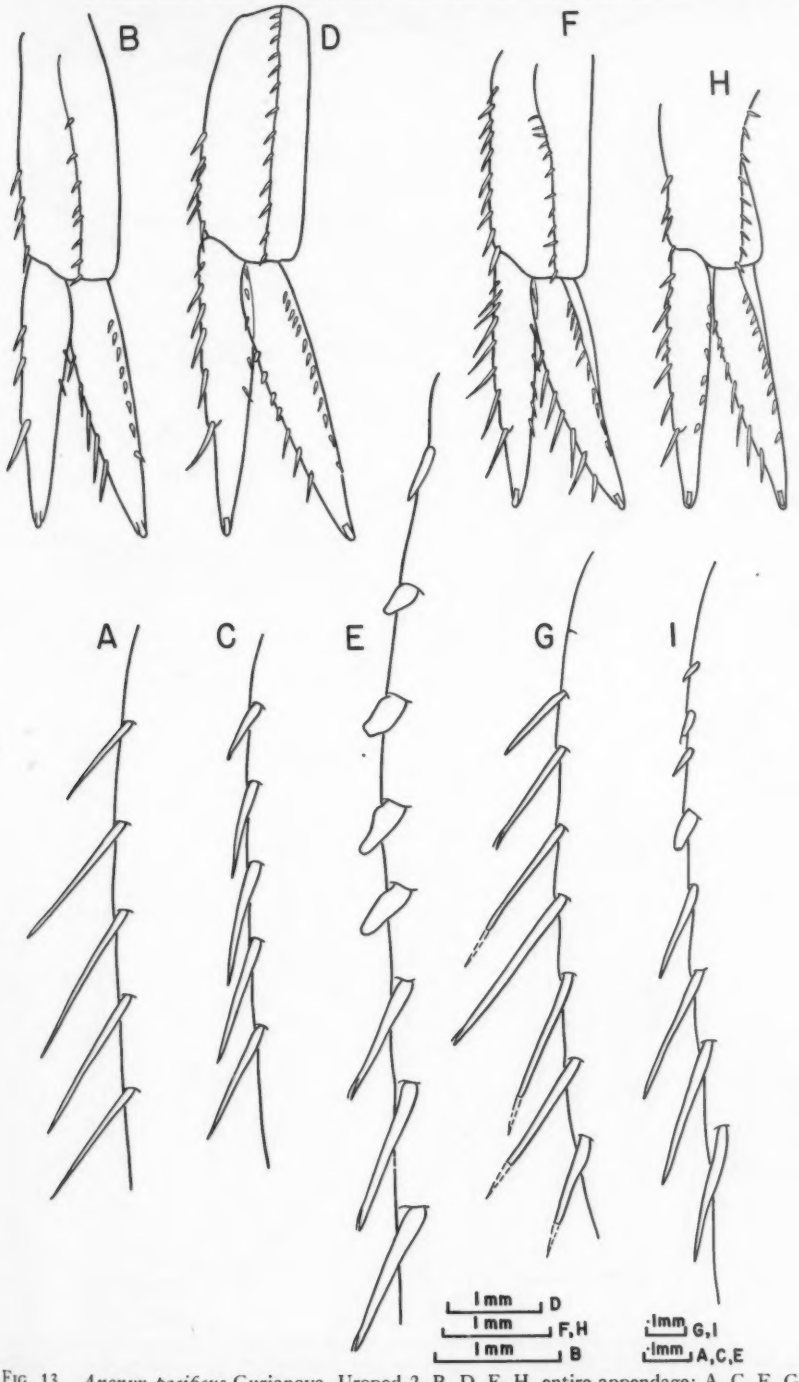

FIG. 13. *Anonyx pacificus* Gurjanova. Uropod 2. B, D, F, H, entire appendage; A, C, E, G, I, inner edge of outer ramus. A, mature female, 32.5 mm, Schooner Harbour, Hudson Strait; B, C, immature male, 25.5 mm, Igloolik Island, Foxe Basin; D, E, mature male, 33 mm, Murray Maxwell Bay, Foxe Basin; F, G, immature male, 26 mm, Sea of Okhotsk; H, I, mature male, 28 mm, Sea of Okhotsk.

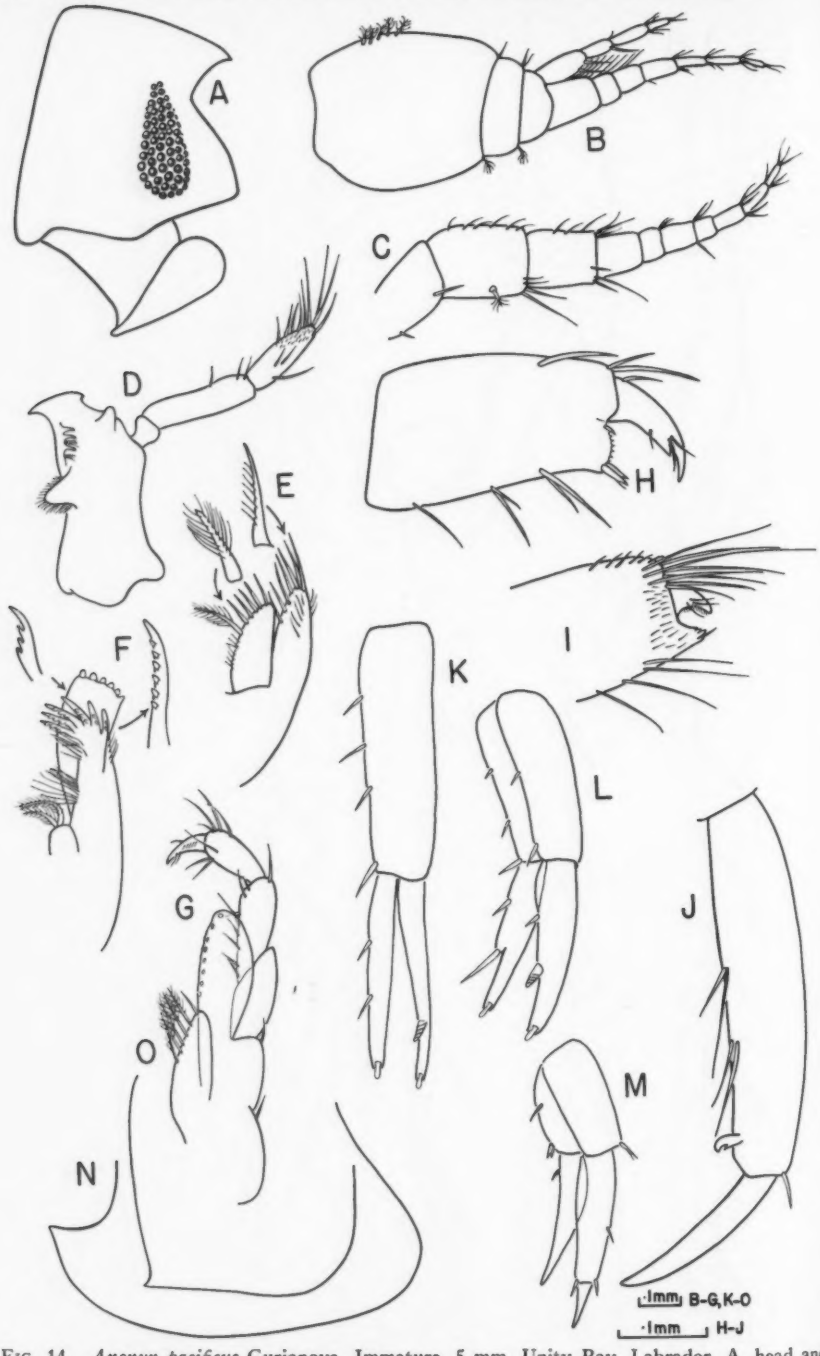

FIG. 14. *Anonyx pacificus* Gurjanova. Immature, 5 mm, Unity Bay, Labrador. A, head and upper lip; B, antenna 1; C, antenna 2; D, right mandible; E, maxilla 2; F, maxilla 1; G, maxilliped; H, peraeopod 1; I, peraeopod 2; J, peraeopod 3; K, uropod 1; L, uropod 2; M, uropod 3; N, lateral plate of third metasome segment; O, lateral plate of second metasome segment.

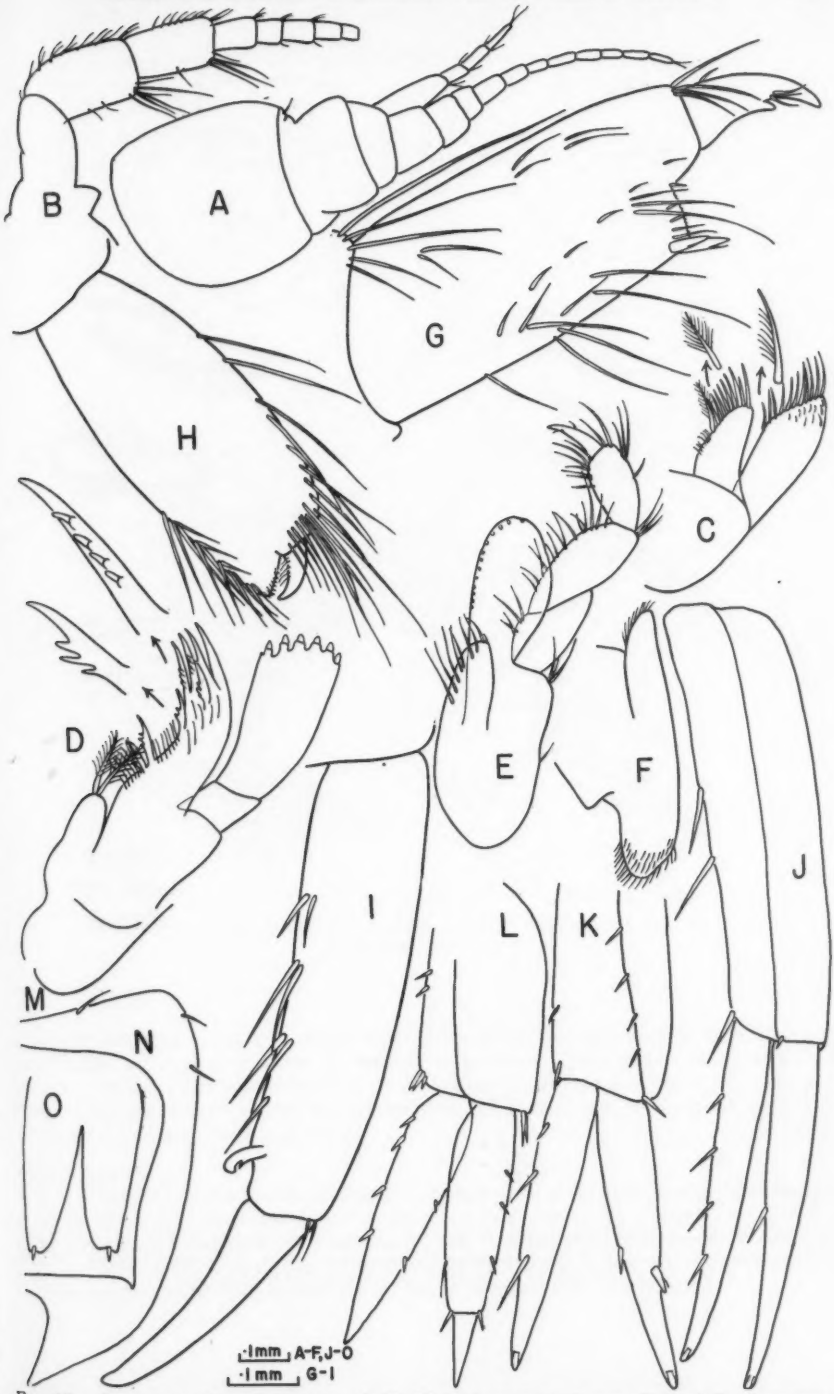

FIG. 15. *Anonyx pacificus* Gurjanova. A–H, M–O, immature, 8 mm, Gulf of St. Lawrence; I–K, immature, 9 mm, Gulf of St. Lawrence. A, antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, maxilliped; F, lower lip; G, peraeopod 1; H, peraeopod 2; I, peraeopod 3; J, uropod 1; K, uropod 2; L, uropod 3; M, lateral plate of third metasome segment; N, lateral plate of second metasome segment; O, telson.

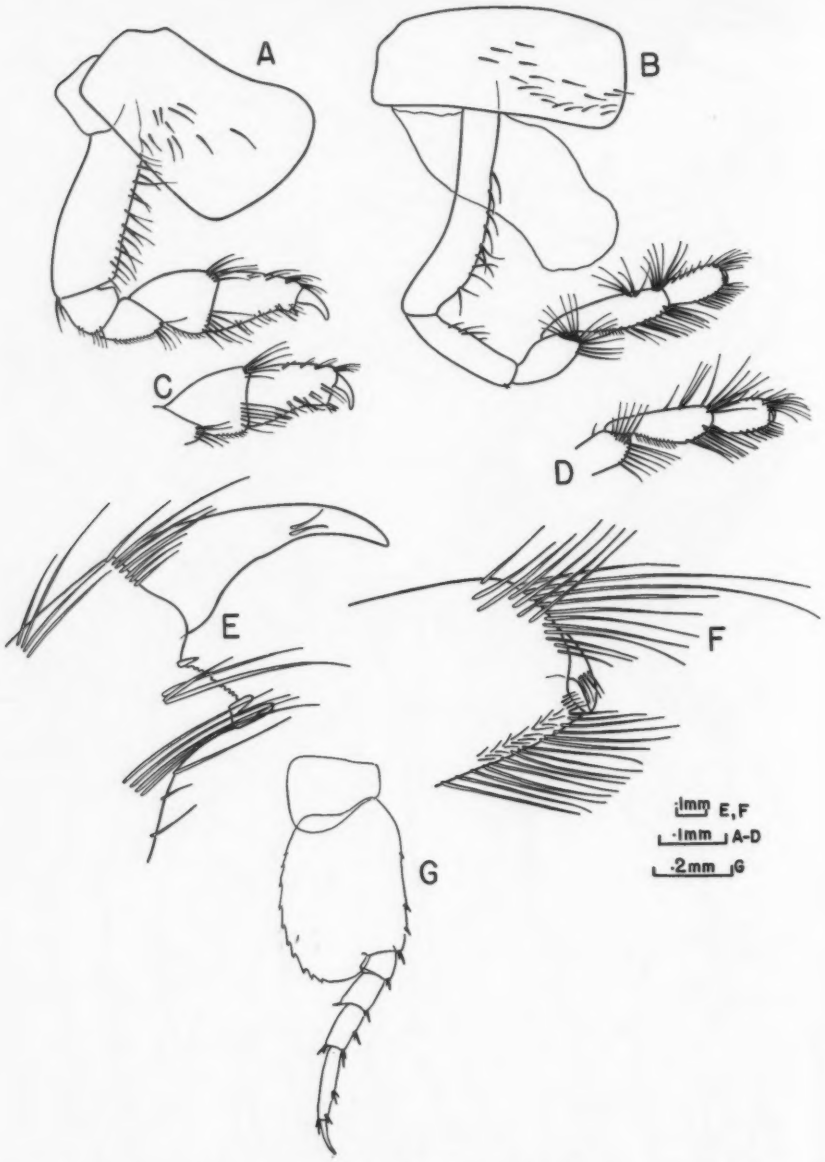

FIG. 16. *Anonyx pacificus* Gurjanova. A, B, E, F, mature male, 28 mm, Sea of Okhotsk; C, D, mature male, 28 mm, Gulf of St. Lawrence; G, immature, 5 mm, Baie des Chaleurs, D112N; A, C, E, peraeopod 1; B, D, F, peraeopod 2; G, peraeopod 7.

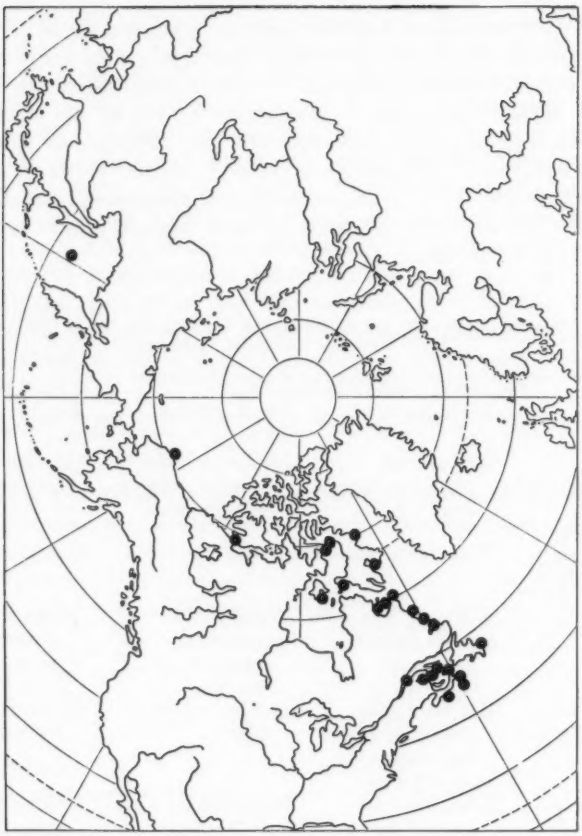

FIG. 17. Distribution of *Anonyx pacificus* Gurjanova based on examined material.

a longer on the other, and these are inserted near the middle of the ramus until there are two spines on the edge. In the first character, *A. pacificus* resembles *A. lilljeborgi* but may be separated from this species by the prominent tooth on the lower posterior corner of the second metasome lateral plate, and also by the coarser denticulation of the hind edge of the basal segment of peraeopod 7 (which is like that of *nugax*).

TYPE-SPECIMEN

We have been unable to find out whether type-specimens of this species, originally described as a subspecies, have been designated. As explained below, the original figures illustrate two rather different specimens, one from the Sea of Japan and the other from the Sea of Okhotsk. Since the latter seems more similar to our little-varying material from many widely distributed localities, we are provisionally considering the Sea of Okhotsk as the type-locality.

VARIATION

Gurjanova (1962) described this form as a subspecies of *A. nugax*, but our examination of specimens from North America waters leads us to believe that it is a separate species, although we acknowledge that it is very closely related to *A. nugax*. The shape of the upper lip, and of the lateral plates of the third metasome segment, and especially the armature of the uropods in the mature male, easily distinguish it from *A. nugax*. However, there are a number of differences between our material and the descriptions of Gurjanova (1962) (Table IV) and it is not without some hesitancy that our specimens are referred to *A. pacificus*.

TABLE IV. Comparison of *Anonyx pacificus* from the Sea of Japan, Sea of Okhotsk (Gurjanova, 1962), and the Northwest Atlantic.

	Sea of Japan	Sea of Okhotsk	Northwest Atlantic
Lateral plate of metasome segment 1	With anterior projection, without setae	Straight, without anterior projection, without setae	With anterior projection, setose
Second segment of mandibular palp	Wider in the middle	Cylindrical	Cylindrical
No. of pairs of dorsal spines on the telson	7	3	3
Rami of uropod 3	Widest at the middle, setose on inner edges only	Widest at the proximal ⅓, setose on both margins	Widest at the proximal ⅓, setose on inner edges only
Constriction of inner ramus of uropod 2	Just beyond the middle (except in the figure of the juvenile male)	Just beyond the middle	Well beyond the middle
Proximal spines on inner margin of inner ramus of uropod 2	Short, less than one-half the distal	Medium-size, slightly more than one-half the distal	Medium-size, three-quarters of the distal
Palm of peraeopod 2	Straight	Concave	Concave

It seems possible that Gurjanova has based her descriptions on specimens of more than one species, since she describes and illustrates in her figures major differences between specimens from the Sea of Okhotsk and others from the Sea of Japan. The specimens from the northwestern Atlantic share several important characters of both forms but differ in others (Table IV). It is apparent that they resemble most closely the specimens from the Sea of Okhotsk. Fortunately, it has been possible to examine specimens from the Sea of Okhotsk that are obviously conspecific with those of the northwestern Atlantic. Even they, however, differ from the Atlantic specimens in that uropod 2 has more and longer spines on the rami, the constriction of the inner

ramus is even more distal, segment 6 of peraeopod 1 is more attenuated distally, segment 6 of peraeopod 2 is relatively longer, and the second segment of the mandibular palp is shorter and slightly expanded in the middle. These differences are all slight, may vary with the size of the specimens and are certainly not enough to consider placing the Atlantic populations in a separate species. However, it is also obvious that our specimens from the Sea of Okhotsk differ from the description of Gurjanova (1962) for specimens from that area and possibly represent a distinct species. They have in fact a resemblance to *A. makarovi* Gurjanova (1962). These problems, as well as the status of the specimens from the Sea of Japan described by Gurjanova (1962), can only be resolved by the examination of more specimens from the Pacific. It is hoped that the detailed description and figures presented here will at least serve to establish the identity of the Atlantic specimens and our specimens from the Sea of Okhotsk, so that later authors will be able to determine its synonymy.

As in *A. nugax*, the size at maturity increases from south to north (Table V) and the larger northern specimens have a better development of spines and setae.

TABLE V. Size (mm) at maturity of *Anonyx pacificus* in different areas.

	Male		Female	
	Maximum size of immature individuals	Size-range of mature individuals	Maximum size of immature individuals	Size-range of mature individuals
Sea of Okhotsk	28	28	–	–
Foxe Basin	28	32–33	34	–
Ungava Bay	–	27–30	32	33
Gulf of St. Lawrence	28	24–31	29	27–32

DISTRIBUTION

The distribution of this species is interesting in that it has so far been recorded from Baffin Island westward to the Sea of Okhotsk and possibly the Sea of Japan, but not from western Greenland and the eastern Atlantic. Even though it has been recorded across the Canadian Arctic Archipelago, it is evidently not common in the Arctic where it is outnumbered by *A. nugax*. However, it is the common large species in the cold intermediate water layer of the Gulf of St. Lawrence. The species has been found as far south as the Nova Scotian banks. The distribution appears, therefore, quantitatively more southern, although it is more decidedly linked with cold water, than that of *A. nugax*. It seems probable that this species has only recently evolved from *A. nugax*, possibly in the warmer waters of the North Pacific, where the specimens apparently diverge more from *A. nugax*, and has emigrated to the northwestern Atlantic across North America only recently, and thus has not yet reached western Greenland.

Anonyx sarsi n.sp.

SYNONYMY

?*Anonyx pallidus* Stimpson, 1853, p. 50; Bate, 1862, p. 81 (*nomen oblitum*).

Anonyx lagena — Schneider, 1884, p. 60; Sars, 1895, p. 686; Stebbing, 1906, p. 54 (not *A. lagena* Krøyer, 1838a).

Anonyx nugax — G. O. Sars, 1891, p. 88, pl. 31; Holmes, 1906, p. 472, 1 fig., pl. III, fig. 3 (not *A. nugax* Phipps, 1774).

DIAGNOSIS OF MATURE FEMALE

Medium-size, peduncle of antenna 2 with tufts of dorsal setae on fourth and fifth segments, upper lip very low and slightly produced, segment 6 of peraeopod 1 slightly narrowed distally, dactyl of peraeopod 1 with an accessory tooth, dactyl of peraeopod 2 small, hind edge of segment 6 of peraeopods 3 and 4 with a single row of long setae paired with a row of long spines, segment 2 of peraeopod 7 shorter than the rest of the limb, hind edge with serrations on distal half, more crowded but not more prominent than proximal ones, inner ramus of uropod 2 slightly constricted and bearing a medium-size spine at the level of the constriction, outer ramus with small similar-size spines on the proximal two-thirds of its inner edge, posterior projection of the lateral plate of the third metasome segment with an evenly rounded convex ventral margin.

DESCRIPTION OF MATURE FEMALE

Maturity is reached at a size of 20–31 mm.

Head.—Shorter than the first two segments of the mesosome. Interantennal lobe rounded, lower margin straight. Eye very large and broad, expanded at the bottom to occupy most of the interantennal lobe, black.

Antenna 1.—Peduncle large, equal in length to the head, first segment longer than it is high, dorsal profile convex. Flagellum short, the first two segments and the third segment of the peduncle with paired or single short spines on their medial surface.

Antenna 2.—With an inner row of feathery setae and a short outer row of long setae on the lower edge and usually three or four bunches of setae on the dorsal edge of the fourth segment of the peduncle. Fifth segment with three groups of setae on the lower edge and on the dorsal edge a few groups of setae which are less distinctly separated than those of segment 4. Flagellum short, with long ventral setae.

Upper lip.—Projecting only slightly in front of the epistome in an evenly rounded lobe, the distal diameter (or height) of which is distinctly smaller than it is in *A. nugax*.

Right mandible.—A single large tooth on the cutting edge. Three spine-teeth and three to five hairly setules in the spine row. Palp, second segment cylindrical and longer than the third; the latter hairy on the anterior surface and with long distally plumose setae.

Left mandible.—Two teeth on the cutting edge.

Maxilla 1.—Outer lobe bearing six short spines and five longer spines each with one to three accessory spines on their distal margin. Palp broadly expanded at the tip and bearing seven conical acute socketed teeth on widely spaced stalks, and one minute unsocketed tooth on the inner corner.

Peraeopod 1.—Coxal plate setose medially and expanded anteriorly into a rounded lobe, maximal width shorter than the height below the antero-proximal corner. Segment 6 equal in length to segment 5 and slightly narrowed distally. Palm perpendicular and defined by two stout spines with accessory hair. Dactyl slightly longer than the palm, with one or two accessory teeth and some setae on the inner margin.

Peraeopod 2.—Segment 6 half as long as segment 5, covered distally and ventrally by long setae with a forked tip and a pectinate medial margin; palm straight or slightly concave and produced slightly under the small finger which is finely setose and distally pectinate and denticulate on its inner margin.

Peraeopods 3 and 4.—Posterior edge of segment 6 with a single row of long setae and a row of long spines paired with the setae; blunt spine at the posterior corner of the sixth segment narrowed and hooked at the apex and lacking an accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with more than 20 serrations, those of the distal half distinctly more crowded and prominent than the proximal ones; maximal length of the segment distinctly shorter than the remainder of the limb.

Branchial vesicles.—Those of peraeopods 2–6, transversely pleated into ridges on both surfaces; of peraeopod 7, unpleated; of peraeopods 5 and 6 with an accessory lobe.

Metasome segment 1.—Anterior edge of the lateral plate setose and produced at the lower corner.

Metasome segment 2.—Lateral plate setose on the anterior and ventral edges, lower posterior corner produced into a prominent acute tooth.

Metasome segment 3.—Not carinate dorsally, lateral plate setose ventrally and anteriorly, posterior projection moderately long, produced into a moderately acute tip with an evenly convex or straight ventral margin.

Urosome segment 1.—Slightly carinate dorsally and projecting slightly posteriorly.

Uropod 1.—Rami almost equal, with small spines (none of which are ridged) on their inner and outer edge.

Uropod 2 (*Fig. 4*).—Rami almost equal. Inner ramus slightly constricted just beyond the middle and bearing a medium-size spine at the level of the constriction. This spine is twice as long as the two or three short proximal spines and its length is one-fifth to one-sixth of the distance from it to the end of the ramus. Outer edge of the inner ramus with a few (1–2) small spines; inner and outer edges of the outer ramus with small spines of similar size, those of the inner margin not extending into the distal third of the ramus; none of these spines are ridged but may possess an accessory hair near their tip.

Uropod 3.—Rami broad and tapering from the anterior third; inner edges with long plumose setae, inner and outer edges with short spines. Outer ramus with a short second segment (one-eighth of the length of the proximal), longer than the inner ramus, and with a few spines on its ventral surface.

Telson.—Deeply cleft, with a single spine inserted in a notch on each apex, and three small spines and a pair of setae on the dorsal surface of each lobe.

Mature Male

The mature male is generally similar to the female except that the antennae are longer and composed of more and longer segments bearing calceoli, the dorsal setae on segment 4 of antenna 2 are in a continuous row, the eyes are usually larger and occupy more of the interantennal lobe (which may be more rounded) than in the female, and the inner edge of the outer ramus of uropod 2 is serrated, with a short blunt spine inserted in each notch. It is in this species that males with the most enlarged eyes (Fig. 18A) are most common in the material that we have examined. Whereas mature males do not always have markedly enlarged eyes (e.g. Cape Fullerton, Hudson Bay, 1904), conversely the largest eyes are not confined to mature males (e.g. submature males from Georges Bank, December 1955). In general, it appears that enlarged eyes are most common in winter and at the southern end (Georges Bank and Woods Hole) of the distribution range, and later (April–June) farther north (Bay of Fundy, Gulf of St. Lawrence).

Young

Early stages of embryos and newly hatched young found in the brood pouch of mature females (Table VI) are similar in size and virtually indistinguishable from those of *Anonyx nugax*.

Specimens 5–6 mm long closely resemble young *A. nugax* and *A. pacificus* and may be distinguished only with difficulty. The long spines on the hind edge of the sixth segment of peraeopods 3 and 4 are not obviously different from the short inner setae of the latter species at this size, but they are a little shorter and always straight and with practice they may be recognized with confidence. In addition, the upper lip is also less produced in *A. sarsi*. The inner ramus of the second uropod is similar to that of *A. nugax* and bears its constriction near the middle, but even at this size the spine at the constriction is relatively shorter (less than one-third of the distance from its insertion to the end of the ramus). In peraeopod 7, the relative lengths of the second segment and the rest of the limb are the same, as they are in *nugax*, and the posterior

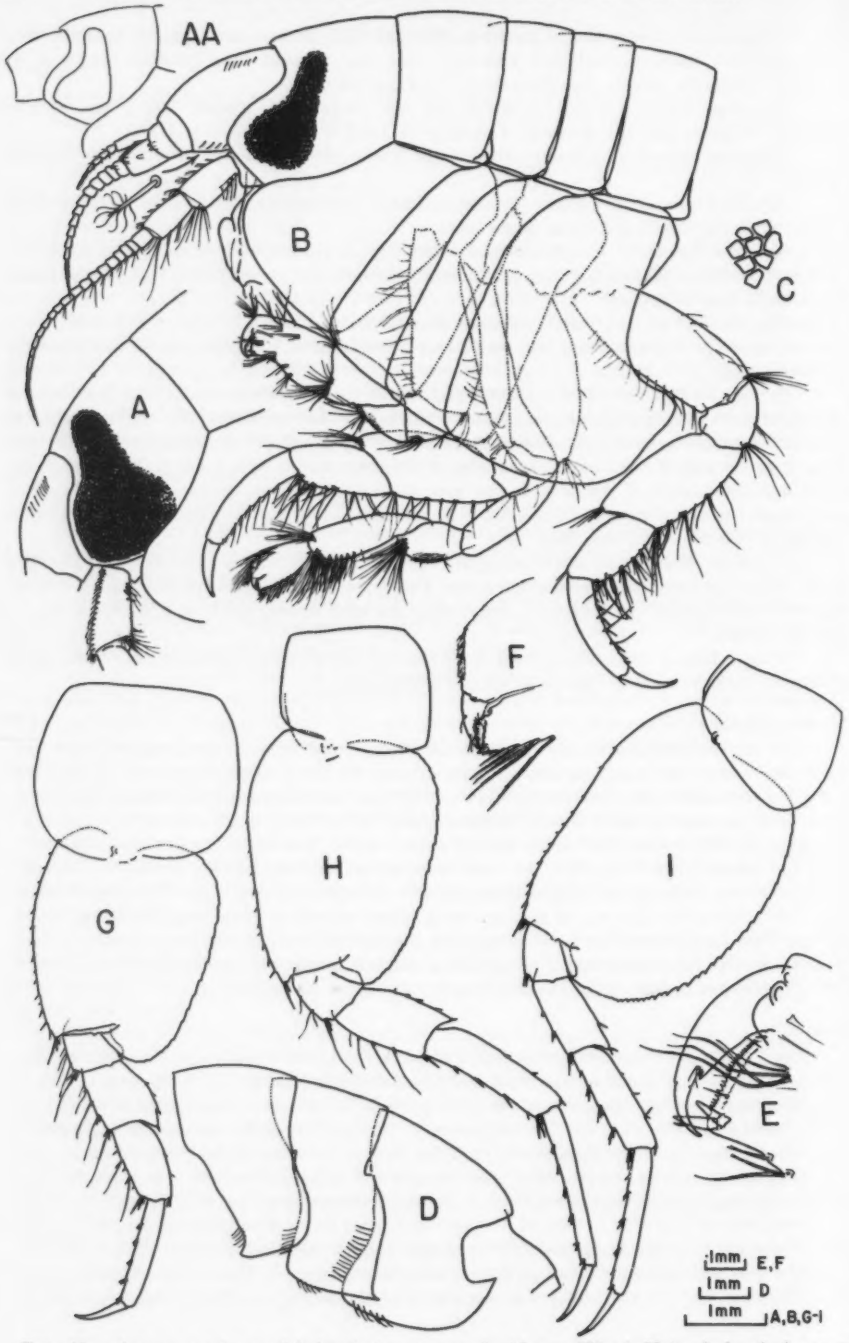

FIG. 18. *Anonyx sarsi* n.sp. AA, head of mature male, 18 mm, Woods Hole; A, head of mature male, 20 mm, Matamek River, Gulf of St. Lawrence; B–I, holotype, immature female, 22 mm, Matamek River; B, anterior; C, sculpturing; D, metasome; E, peraeopod 1; F, peraeopod 2; G, peraeopod 5; H, peraeopod 6; I, peraeopod 7.

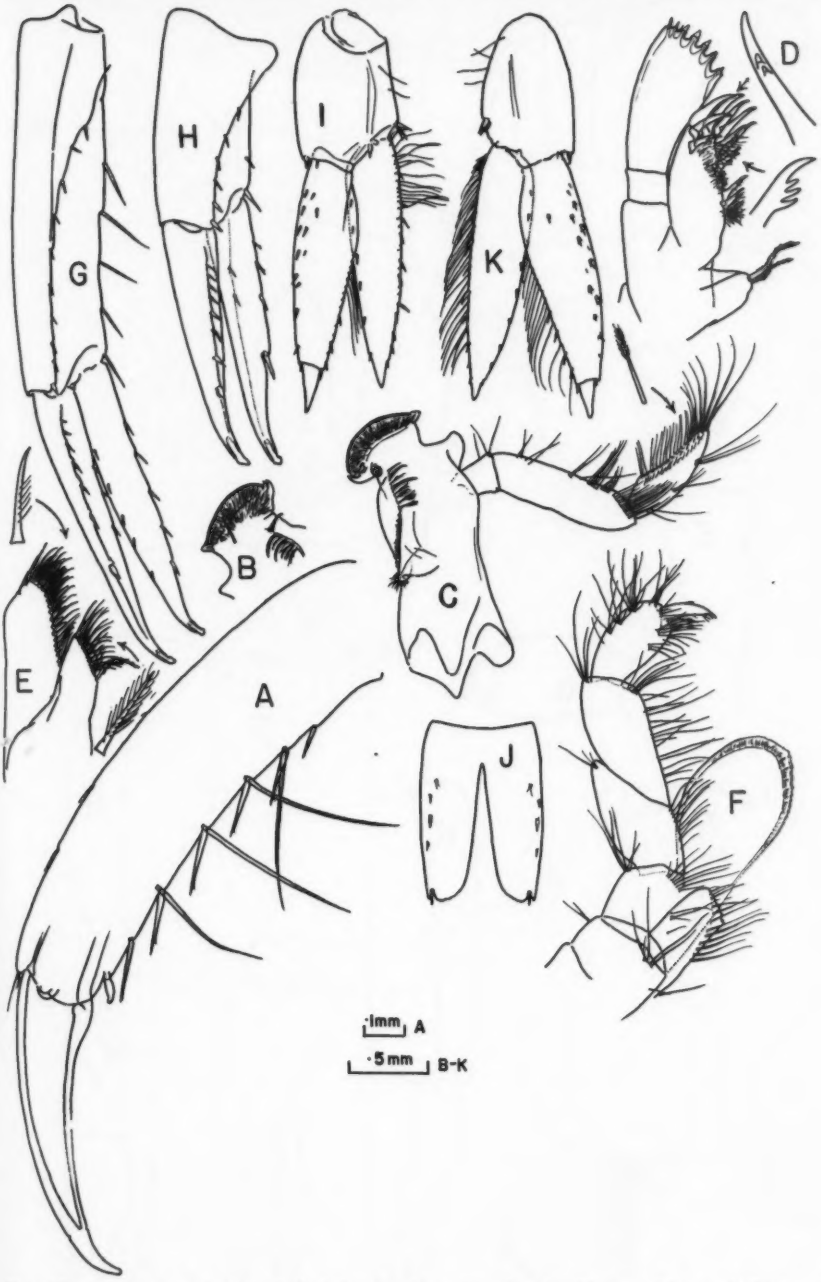

FIG. 19. *Anonyx sarsi* n.sp. A–J, holotype, immature female, 22 mm, Matamek River; A, peraeopod 3; B, left mandible; C, right mandible; D, maxilla 1; E, maxilla 2; F, maxilliped; G, uropod 1; H, uropod 2; I, uropod 3; J, telson; K, uropod 3 of mature male, 18 mm, Woods Hole.

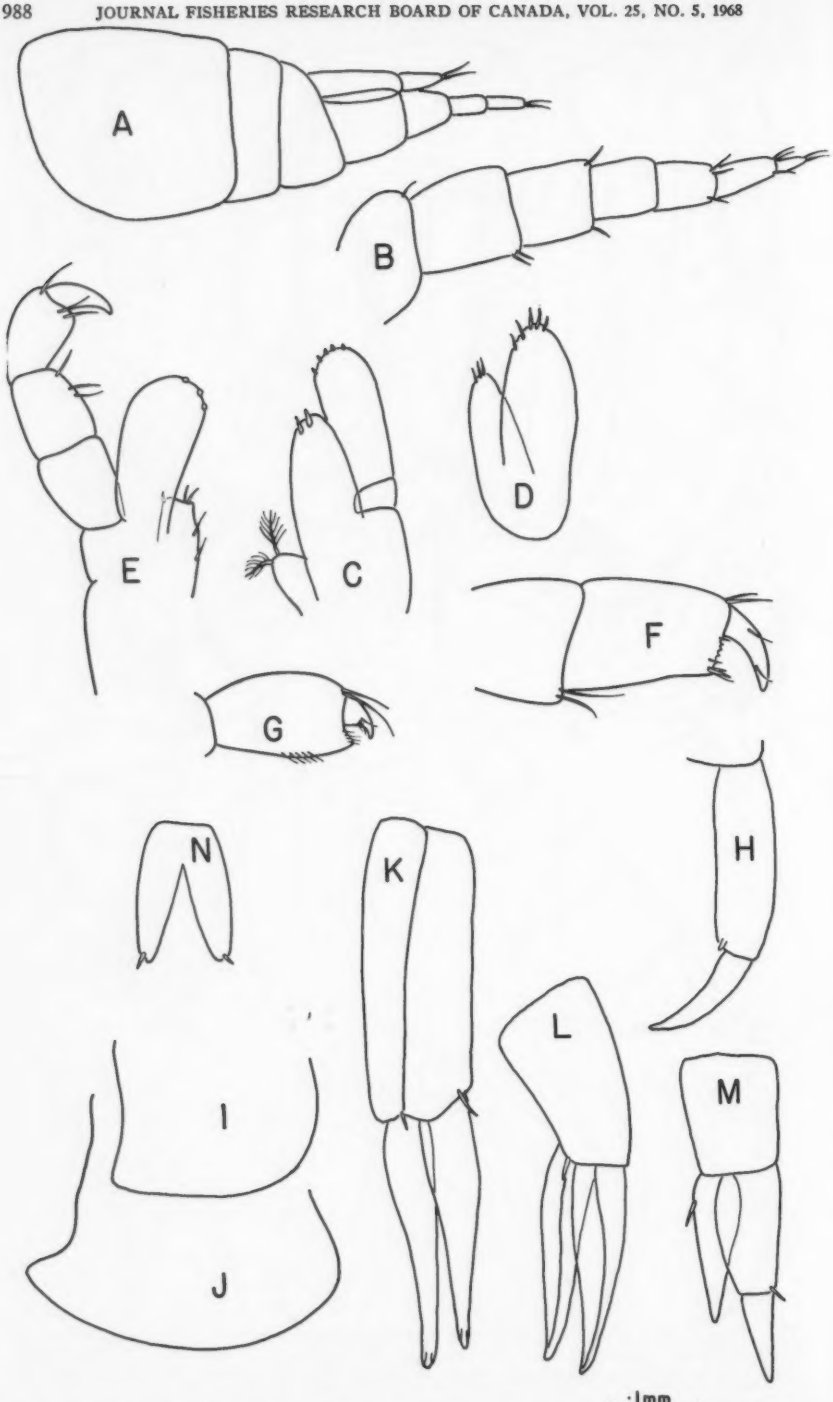

FIG. 20. *Anonyx sarsi* n.sp. Immature, 3 mm, from brood pouch of 28-mm female from Pt. Burwell, Ungava Bay. A, antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, maxilliped; F, peraeopod 1; G, peraeopod 2; H, peraeopod 3; I, lateral plate of second metasome segment; J, lateral plate of third metasome segment; K, uropod 1; L, uropod 2; M, uropod 3; N, telson.

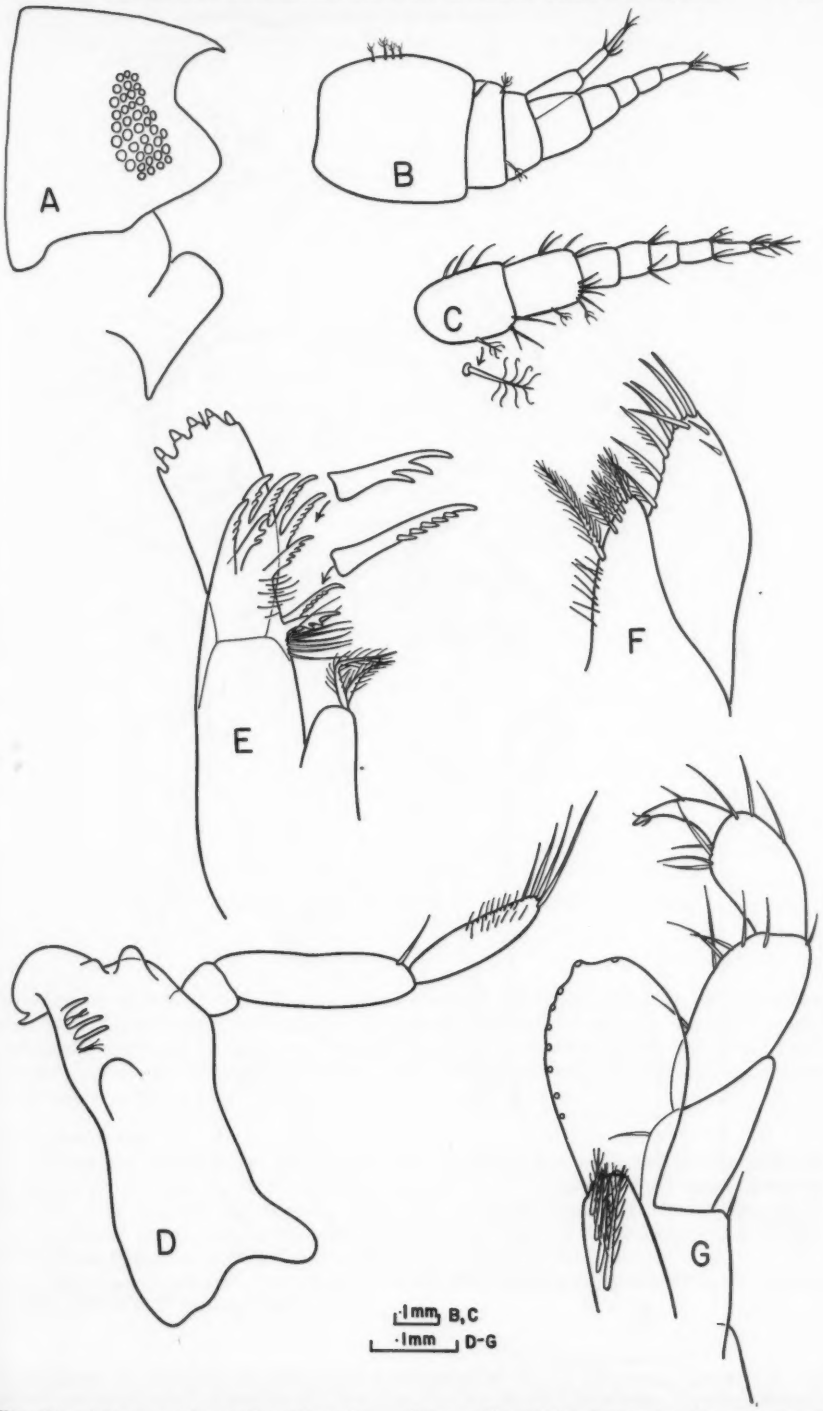

FIG. 21. *Anonyx sarsi* n.sp. Immature, 5 mm, Ungava Bay. A, head and upper lip; B, antenna 1; C, antenna 2; D, right mandible; E, maxilla 1; F, maxilla 2; G, maxilliped.

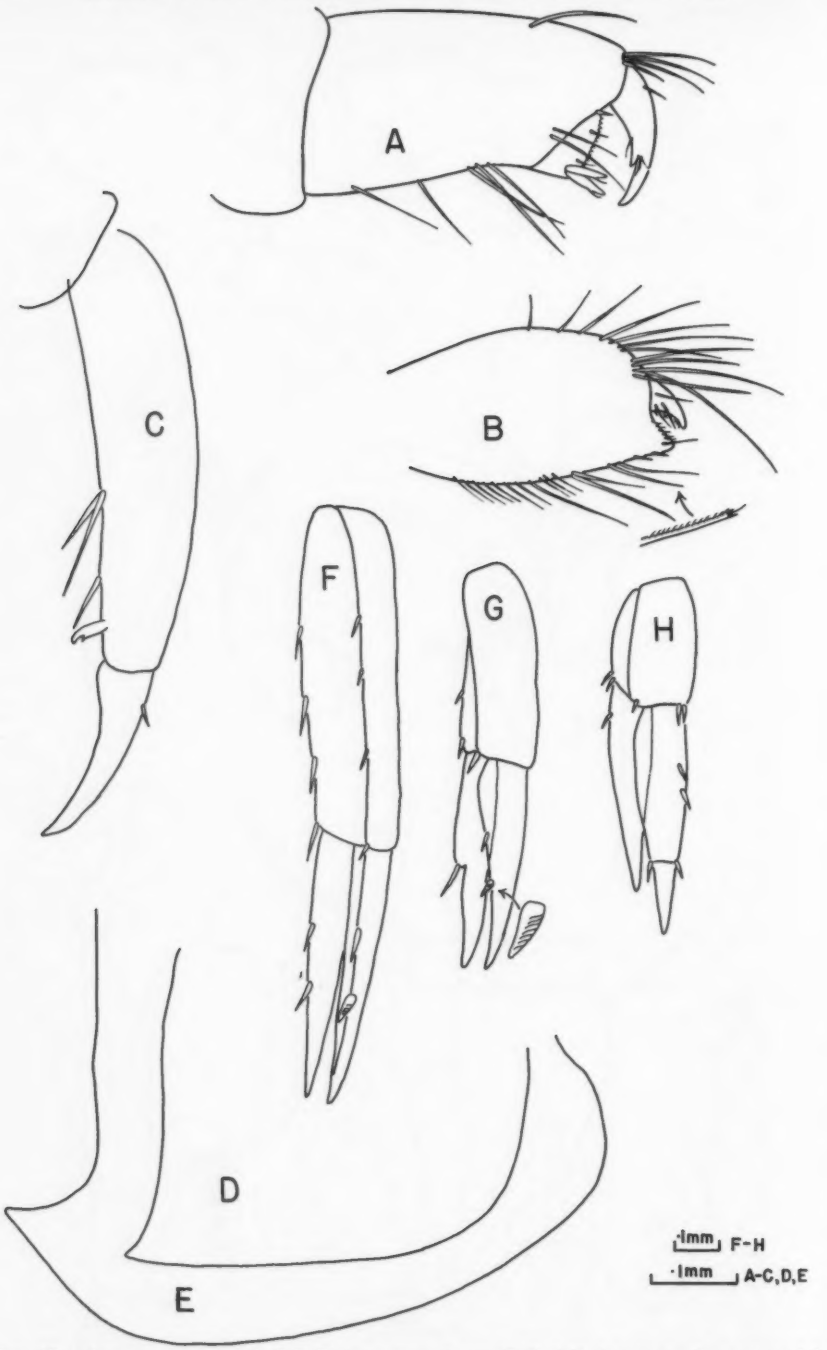

FIG. 22. *Anonyx sarsi* n.sp. A–C, F–H, immature, 6 mm, Gulf of St. Lawrence. A, peraeopod 1; B, peraeopod 2; C, peraeopod 3; F, uropod 1; G, uropod 2; H, uropod 3; D, E, immature, 5 mm, Ungava Bay; D, lateral plate of second metasome segment; E, lateral plate of third metasome segment.

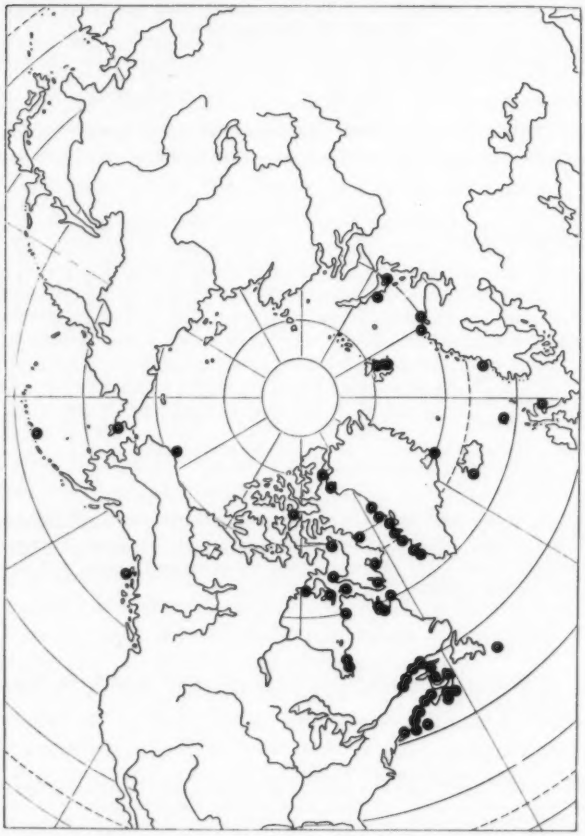

FIG. 23. Distribution of *Anonyx sarsi* n.sp. based on examined material.

serrations of segment 2, which are of some use in the adult, appear to be variable, being sometimes like those of small *nugax*, sometimes less prominent. The tufts of setae on the dorsal edge of peduncular segment 4 of the second antenna also occur in juvenile females and males at least as small as 8 mm but, especially in the latter, they are less distinctly separated and the proximal tuft may be in fact a small row.

TYPE-SPECIMENS

Holotype: immature female, 22 mm, with developing but nonsetiferous oostegites. Off Matamek River, about 50°30′N, 65°59′W, June 18–21, 1927, collected by Copley Amory and Paul Bowman, No. 219 (see Bartsch, 1928). The specimens were most probably collected in shallow coastal waters, judging from the limited seagoing means of the field-party. U.S. National Museum, accession No. 95922, Cat. No. 103666 (one vial, one slide).

Allotype: mature male, 22 mm, with calceoli, from same sample. U.S. National Museum, same numbers (one vial, one slide).

TABLE VI. Sizes of early embryos and hatched young from the brood pouch of ovigerous females of *Anonyx sarsi*.

Locality	Size of female (*mm*)	No. measured	Length (*mm*)		Diam (*mm*)	
			Mean	Range	Mean	Range
Early embryos						
Vadsö, Finmark	20	1	1.3	–	1.1	–
Port Burwell, Ungava Bay	25	3	1.3	0.9–1.3	1.1	1.2–1.3
"	28	6	1.4	1.2–1.5	1.1	.9–1.3
"	26	2	1.5	1.4–1.5	1.2	1.2–1.3
"	26	3	1.3	1.3–1.4	1.2	1.2
"	28	3	1.5	1.4–1.5	1.3	1.2–1.4
Hatched young						
Port Burwell, Ungava Bay	25	5	2.7	2.6–2.7	–	–
Port Burwell, Ungava Bay	26	5	3.1	2.9–3.1	–	–
Fylla Bank, W Greenland	30	6	3.1	3.0–3.2	–	–

Paratypes (rest of the same sample): one lot of 36 juvenile males, 35 juvenile females with oostegites, and one young female without oostegites: U.S. National Museum. Another lot containing one mature male, three juvenile males, six juveniles females, and one young female without oostegites: National Museum of Canada, Ottawa.

VARIATION

The size at maturity appears to increase from south to north as in the other species (Table VII).

TABLE VII. Size (mm) at maturity of *Anonyx sarsi* in different areas.

	Male		Female	
	Maximum size of immature individuals	Size-range of mature individuals	Maximum size of immature individuals	Size-range of mature individuals
Foxe Basin–Cornwallis Island	–	–	31	–
Hudson Bay and Strait	–	28	–	30
Ungava Bay	26	28	27	25–30
Gulf of St. Lawrence and Estuary	23	20–24	24	25
Nova Scotia banks and Bay of Fundy	–	17–22	–	20
Vineyard Sound and Georges Bank	20	16–21	19	–
Finmark, North Norway	–	–	–	18

REMARKS

This species has apparently not been named previously, in spite of its common occurrence in shallow water and its wide distribution. However, it is possibly the species insufficiently described, without figures, as *Anonyx pallidus* by Stimpson (1853) from a small (about 9 mm) specimen, a species endorsed later by Bate (1862) but removed to the *incertae sedis* by Stebbing (1906) and forgotten since. We quote in extenso Stimpson's description:

"Body short, slightly compressed, rounded above, with a sinus at the abdomen as in *A. politus*. Head with large, black, subclavate eyes, broadest below, as in *A. appendiculosus*, Kr. Antennae hairy, very short, the superior ones very thick and tapering, equalling the inferior ones in length, that is, reaching the second thoracic segment. Legs slender, very hairy, in structure like those of the above species (i.e. *A. politus*). Caudal stylets of the first two pairs long and pointed, slightly serrated above, those of the last pair short, thick, and spinous. Color pale-whitish, the brownish viscera showing through along the middle. Length, 0.35. Taken in four fathoms, in sand, off Duck Island moorings; in ten fathoms off Cheney's Head; and in twenty fathoms, mud and shells, off the northern point of Duck Island."

Anonyx sarsi is probably the only common species of amphipod with such eyes in shallow water in the Grand Manan area, and Stimpson otherwise does not record any other species which might be identified with the common one known then as *A. ampulla* and other names. However, the description of the eye does not entirely exclude *A. lilljeborgi*, the other common *Anonyx* at Grand Manan, and Stimpson describes antenna 2 as having the same length as antenna 1 (whereas it is much longer in *sarsi*). Uncertainty thus remains and a new name for *A. sarsi* is therefore preferable.

On the other hand, *A. sarsi* is probably also the form with the southern distribution discussed by Sars (1895) and placed by him in Krøyer's species *A. lagena*. Unfortunately, to distinguish this form he chose characters (relative lengths of segments 5 and 6 of peraeopod 1) that vary with the size of the specimen and it was therefore soon returned to the synonymy of *A. nugax* by Brüggen (1907). We strongly suspect, moreover, that Sars (1891) used a specimen of *A. sarsi* to prepare his plate 31 illustrating *A. nugax*: the small size (15–18 mm) of his specimen (as shown on the plate), the probable predominance of *sarsi* in Norwegian coastal waters (most Norwegian specimens which we examined, including those determined by Sars, were actually *sarsi*), the convex dorsal profile of antenna 1, and the large eye of the male, provide hints for this belief. *Anonyx sarsi* is also the species described and illustrated by Holmes (1905) under the name *A. nugax*. The enlarged eye of the specimen from Vineyard Sound photographed on plate III, the maximum size (about 20 mm) reported for New England specimens, and the fact that this is the only fairly large inshore species of *Anonyx* in the area, identify Holmes' species as *A. sarsi*.

Anonyx sarsi probably has not been examined critically since Holmes' time. Because the type of *A. lagena* has proved upon examination to be a specimen of what we consider to be a typical individual of *A. nugax*, the present species requires a new name. We propose to name it after G. O. Sars in honour of his earlier recognition that it constitutes a distinct species.

Distribution

Almost all of the collections that we examined came from depths of less than 50 m, suggesting that *A. sarsi* is typically an inhabitant of shallow water and sandy substrates. It is probably circumpolar for it extends from Novaya Zemlya westward to Bering Strait, and in the northwestern Atlantic region it is known from Ellesmere Island and Foxe Basin southward to Rhode Island. However, it does not seem to be common north of Hudson Stait, judging by its low frequency in collections as compared with *A. nugax*.

Anonyx laticoxae Gurjanova, 1962

Diagnosis of Mature Female

Large, interantennal angle of head very rounded, first peduncular segment of antenna 1 with a strongly convex dorsal profile, upper lip produced very slightly, first coxal plate expanded anteriorly into a broad rounded lobe, its maximal width as long as the height below the antero-proximal corner, segment 6 of peraeopod 1 narrowed slightly distally, dactyl without an accessory tooth, dactyl of peraeopod 2 small, hind edge of peraeopods 3 and 4 with a row of long setae and a corresponding row of short thick spines paired with the setae, segment 2 of peraeopod 7 weakly serrated on hind edge, shorter than rest of the limb, inner ramus of uropod 2 not constricted, spines small, inner margin of outer ramus without spines, rami of uropod 3 broad with setae only on the inner margins, second metasome lateral plate with a distinct tooth in the postero-distal corner, posterior projection of the third metasome lateral plate short, evenly rounded ventrally and not particularly acute distally.

Description of Mature Female

This species apparently matures when longer than 30 mm, although few specimens of this size have been collected. Integument is opaque and chalky. It should be noted that, since the single available mature female had lost her pleon, Fig. 24–25 had to be prepared from the next largest specimen at hand, which unfortunately did not come from Atlantic or Arctic regions.

Head.—Shorter than the combined first two segments of the mesosome. Interantennal lobe broadly rounded, lower margin convex. Eye large, narrow at the top (narrowest of all eight species described here), but greatly expanded below to occupy most of the interantennal lobe, posterior margin concave, red-brown in colour.

Antenna 1.—Peduncle large, segment 1 bulbous, higher than it is long, dorsal profile strongly convex. Flagellum short, moniliform, with a pair of short rods (aesthetascs?) on the medial surface of the second segmeht and a single rod on the third segment.

Antenna 2.—With a row of feathery setae on the lower edge and a row of setae on the dorsal edge of the fourth segment of the peduncle. Two groups of setae on the dorsal edge of the fourth segment of the peduncle. Two groups of setae with a few feathery setae on the lower edge and a row of setae on the dorsal edge of the fifth segment. Flagellum short, with short ventral setae.

Upper lip.—Small, projecting very little in front of the epistome as an evenly rounded lobe.

Right mandible.—With a single large tooth on the cutting edge. Five spine-teeth and three to six hairy setules or spinules in the spine row (difficulty in distinguishing spine-teeth from setules is likely). Palp, first segment narrow, second cylindrical and longer than the third; the latter hairy on the anterior surface and with plumose coarse setae on the posterior margin.

Left mandible.—Two teeth on the cutting edge.

Maxilla 1.—Outer lobe bearing six small spines with two to five accessory teeth and five longer spines with one to six accessory teeth. Palp distally expanded and bearing seven to eight

conical socketed teeth on narrowly spaced low stalks except the outermost which is unstalked, and one small unsocketed tooth on the inner corner.

Peraeopod 1.—Coxal plate greatly expanded anteriorly and rounded, maximal width about as long as the height below the antero-proximal corner. Segment 6 longer than segment 5, slightly narrowed distally, palm perpendicular, and defined by two stout spines each with an accessory hair. Dactyl slightly longer than the palm, setose, without an accessory tooth.

Peraeopod 2.—Sixth segment short, about one-third of the length of segment 5, covered distally and ventrally by long setae with a forked tip and a pectinate medial margin. Palm straight or slightly concave and produced under the small dactyl which is finely setose and pectinate and distally denticulate on its inner margin.

Peraeopods 3 and 4.—Posterior edge of segment 6 with a row of setae paired with stout spines. Spine at the posterior corner of the sixth segment distally narrowed, but not hooked and lacking an accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with very indistinct serrations (about 23 on the specimen in Fig. 24), those of the distal half not more projecting and acute than the proximal ones; maximal length of the segment distinctly shorter than the remainder of the limb.

Branchial vesicles.—On peraeopods 2–6, transversely pleated into ridges on both sides; on peraeopod 7, unpleated; on peraeopods 5 and 6, with an accessory lobe.

Metasome segment 1.—Anterior edge of the lateral plate without setae, produced anteriorly at the ventral corner.

Metasome segment 2.—Lateral plate produced into a prominent acute tooth at the posterior corner, anterior edge setose.

Metasome segment 3.—Lateral plate setose anteriorly and ventrally, posterior projection short, evenly rounded posteriorly and extending into a short moderately acute tip with a straight or faintly concave lower edge.

Urosome segment 1.—Slightly carinate dorsally and projecting posteriorly to a slight extent.

Uropod 1.—Rami almost equal, with small marginal spines, none of which are ridged.

Uropod 2.—Rami almost equal and distinctly upturned distally. Inner ramus not constricted, distal spine on the inner edge short, almost equal in length to the proximal spines and one-eighth of the distance from it to the end of the ramus. Outer ramus without spines on the inner edge and short spines on the outer edge.

Uropod 3.—Rami almost equal in length, broad, setose on their inner margin only. Edges of the inner ramus almost parallel, tapering from the distal third. Outer ramus with a short second segment (one-tenth of the length of the proximal), a few ventral spines, and tapering from the proximal third.

Telson.—Deeply cleft, with a single spine in the distal notch of each lobe and three to four dorsal spines and a pair of setae on the dorsal surface.

Mature Male

A single mature male, of rather small size (28 mm), was found in the material at our disposal: it came from Spitsbergen and, together with a large female of *A. nugax*, constitued a lot previously considered as Krøyer's type-specimens of *A. lagena*, but which must now yield this status to the true types from Greenland. The mature male is very much like the female, except that the eyes are larger, although still narrow dorsally, the antennae are longer and composed of more and longer segments bearing calceoli, and metasome segment 3 has a distinct median dorsal carina (a character otherwise present only in *A. ochoticus* among our species).

Young

No ovigerous females with developing embryos or hatched young were found and the smallest specimens identified as this species were 7 mm long. These were generally similar to *A. nugax* of equal size but differed enough to be readily identified as this species.

The upper lip is very small and extends only slightly in front of the epistome. The first segment of the peduncle of antenna 1 is longer than it is deep, with dorsal and ventral rows of feathery setae and a cluster of them at the lower anterior corner. The right mandible is similar

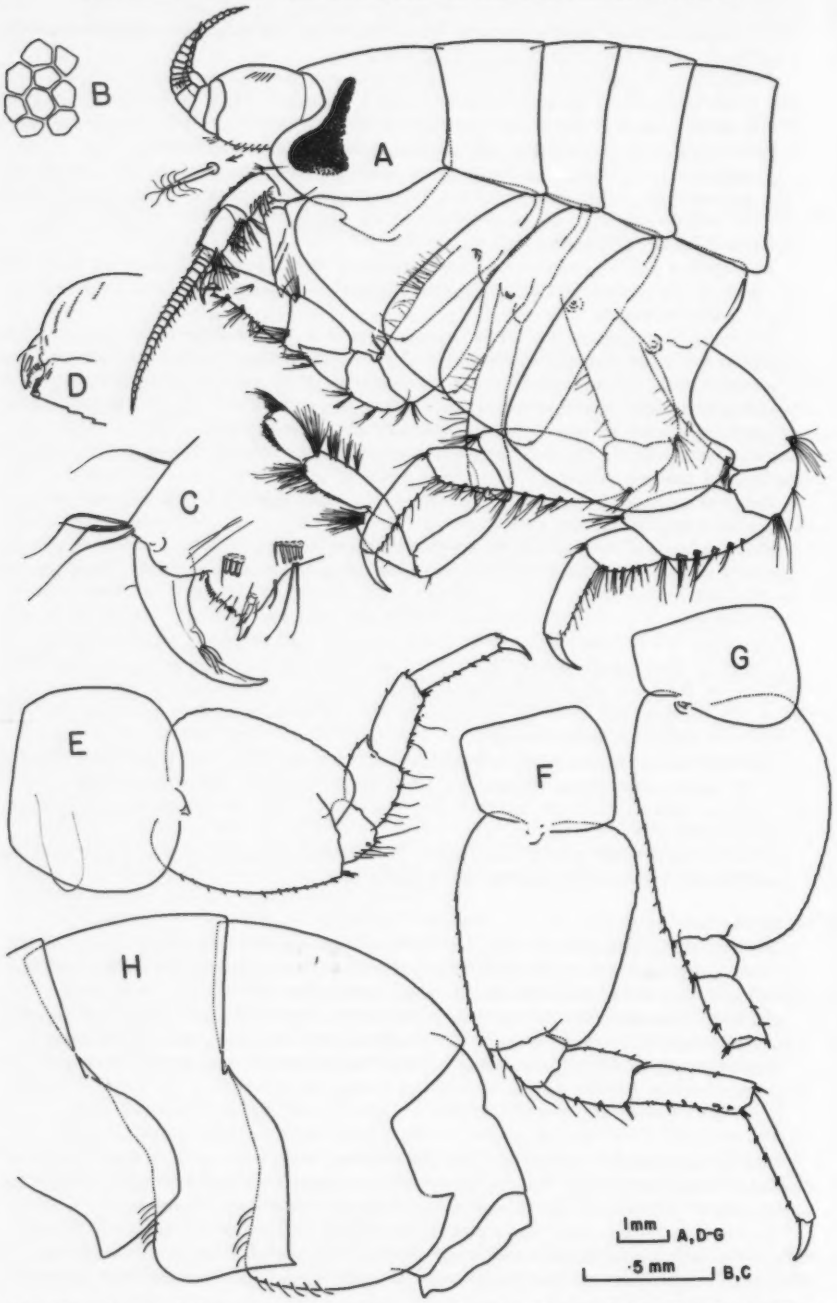

FIG. 24. *Anonyx laticoxae* Gurjanova. Immature female, 33 mm, Indian Pt., Bering Sea. A, anterior; B, sculpturing; C, peraeopod 1; D, peraeopod 2; E, peraeopod 5; F, peraeopod 6; G, peraeopod 7; H, metasome.

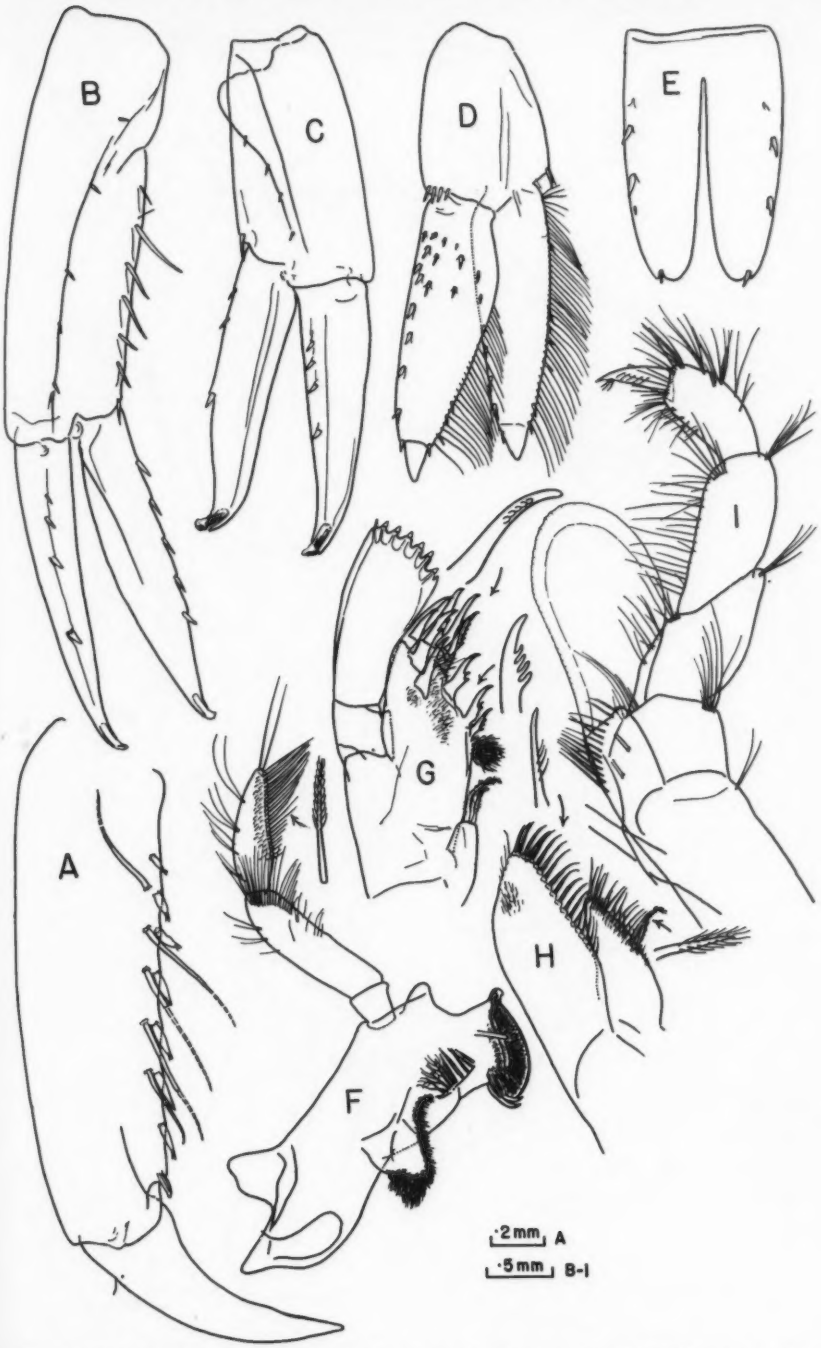

FIG. 25. *Anonyx laticoxae* Gurjanova. Immature female, 33 mm, Indian Pt., Bering Sea. A, paraeopod 3; B, uropod 1; C, uropod 2; D, uropod 3; E, telson; F, left mandible; G, maxilla 1; H, maxilla 2; I, maxilliped.

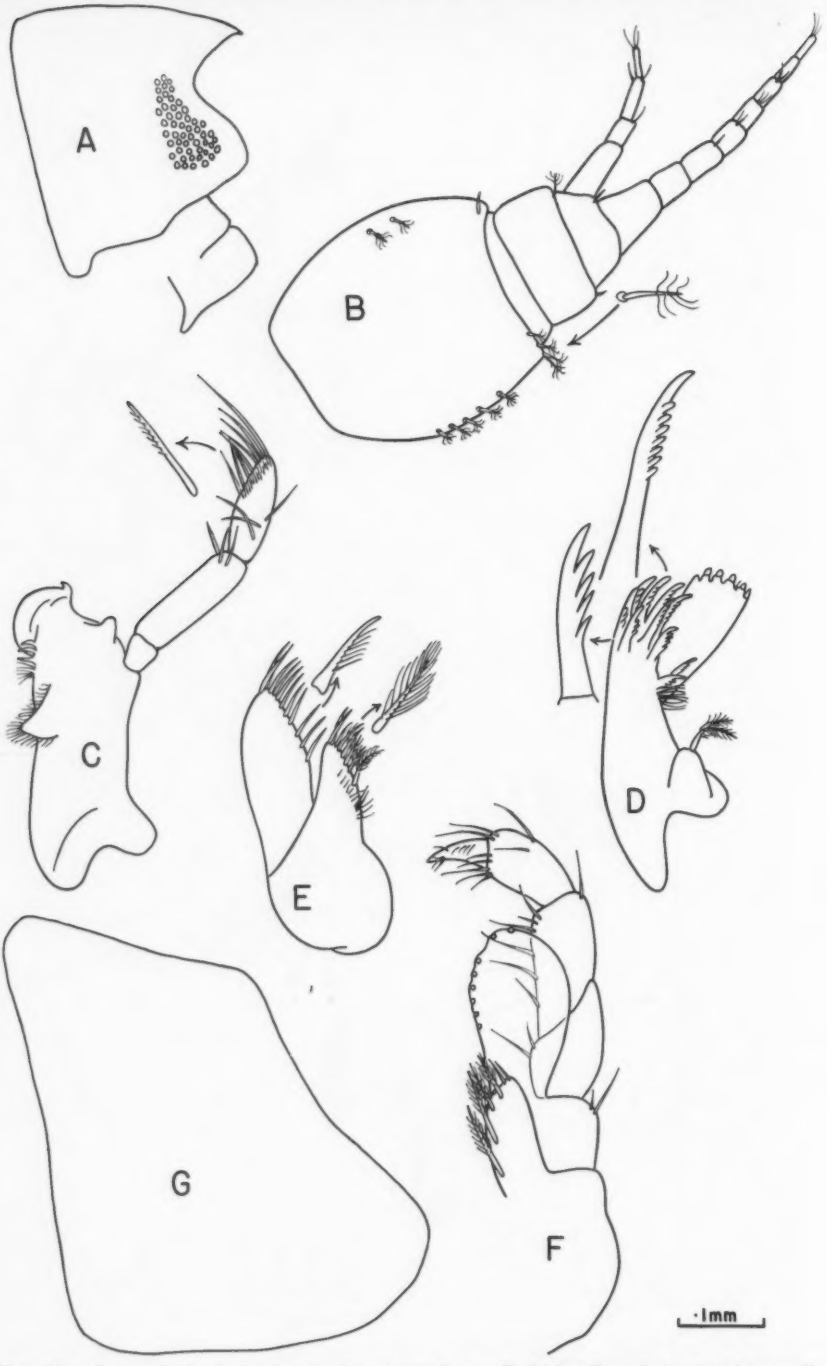

FIG. 26. *Anonyx laticoxae* Gurjanova. Immature, 7 mm, Frobisher Bay. A, head and upper lip; B, antenna 1; C, right mandible; D, maxilla 1; E, maxilla 2; F, maxilliped; G, coxal plate 1.

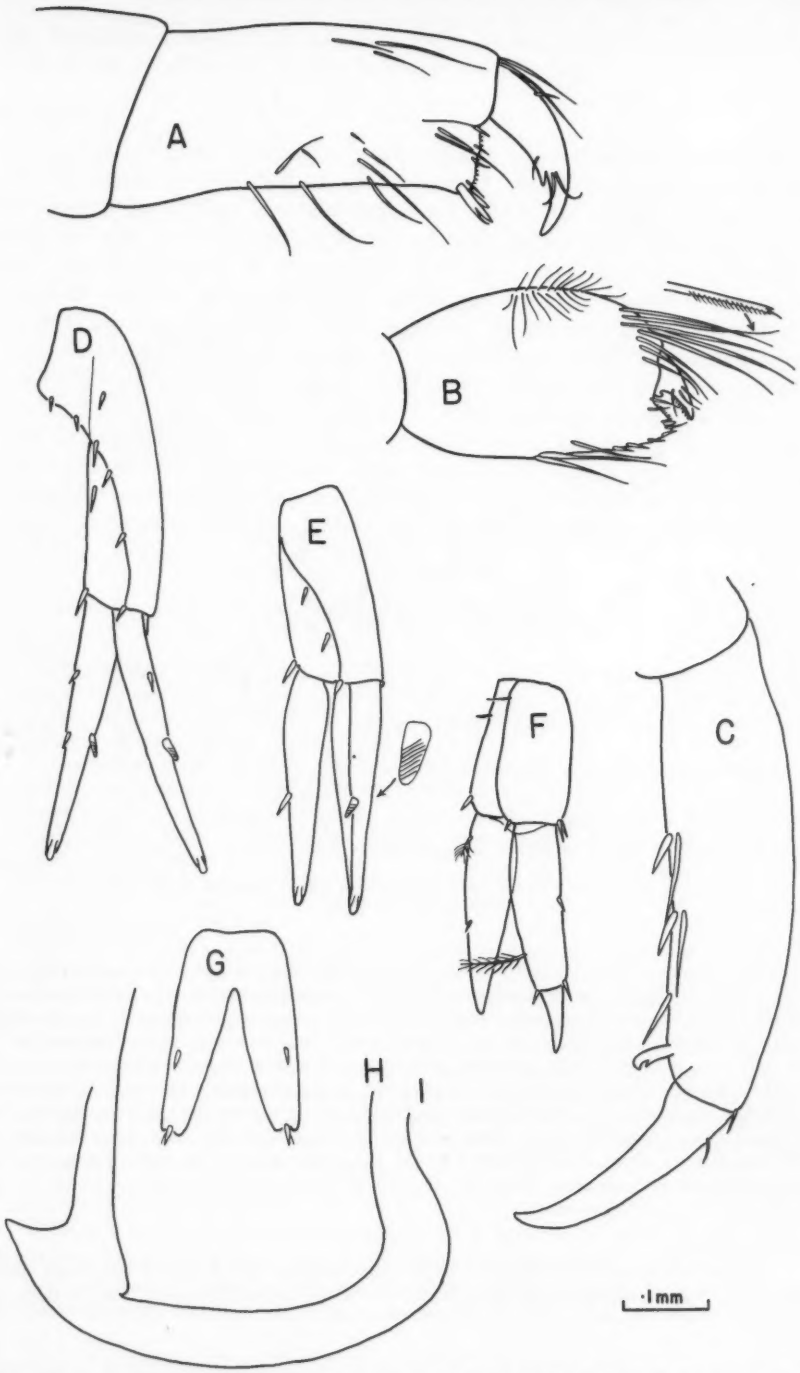

FIG. 27. *Anonyx laticoxae* Gurjanova. Immature, 7 mm, Frobisher Bay. A, peraeopod 1; B, peraeopod 2; C, peraeopod 3; D, uropod 1; E, uropod 2; F, uropod 3; G, telson; H, lateral plate of metasome segment 2; I, lateral plate of metasome segment 3.

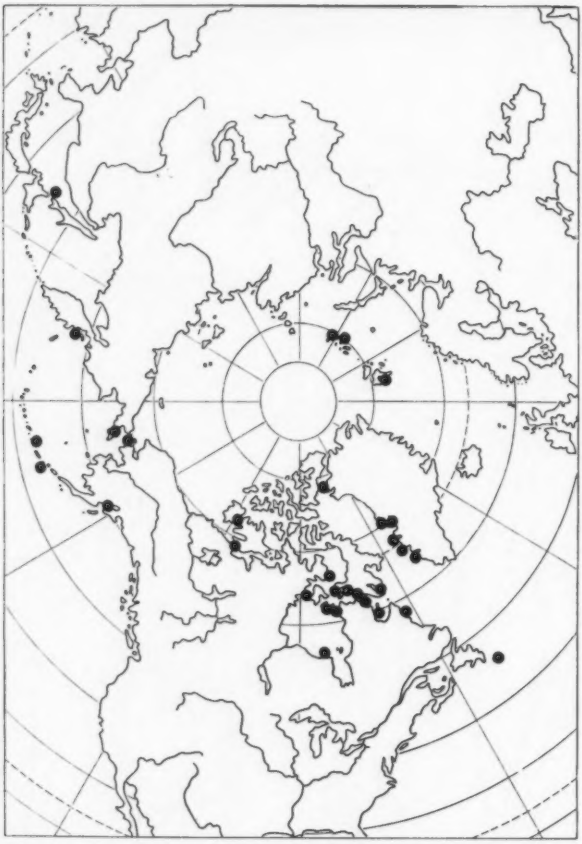

FIG. 28. Distribution of *Anonyx laticoxae* Gurjanova based on examined material.

to that of the adult but with only three spine-teeth in the spine row and a shorter third segment of the palp; the setae on the inner margin of the latter segment are apparently, in animals of this size, distally pectinate on their medial surface rather than plumose. The spines on the outer lobe of maxilla 2 have from four to nine teeth and the second segment of the palp has five socketed teeth. The first coxal plate is broadly expanded anteriorly and already has the same proportions as those of the adult. The stout spines on the hind margin of peraeopods 3 and 4 are obvious even at this size. The distal spines on the outer margins of both rami of uropod 1 and the outer ramus of uropod 2 are ridged. The inner ramus of uropod 2 is not constricted and the distal spine is short (one-quarter of the distance from it to the end of the ramus). The rami of uropod 3 are narrow, with few plumose setae; the second segment of the outer ramus is almost one-half of the length of the proximal segment.

TYPE-SPECIMENS

We have been unable to discover whether type-specimens of this species have been designated. The type-locality (the only one mentioned with the original description) is Paramutchir

Island, Kurile Islands, North Pacific, at a depth of about 150 m, where Gurjanova (1962) says that several individuals ("size 27 mm") of both sexes were collected.

DISTRIBUTION

Anonyx laticoxae is essentially a northern species and its distribution generally coincides with that of cold waters. It has been found only as far south as the Grand Banks of Newfoundland, the latter isolated record being based, however, on a young specimen very badly deprived of diagnostic parts (pleon, sixth segments of peraeopods 3–4), but nevertheless characteristic in its first antenna, first coxal plate, and upper lip. The species is otherwise recorded here from the North Pacific eastward to western Greenland, but the two more-or-less isolated records from Franz Joseph Land and Spitsbergen are a little puzzling because of their relative remoteness from the main western area of distribution. *Anonyx laticoxae* is collected less frequently than *A. nugax* in northern areas, and is apparently less abundant or has a more restricted ecological distribution. This may explain the scarcity of records in the northeastern Atlantic and Siberian waters. On the other hand it may be another example of a species of Pacific origin which has recently spread eastward.

Anonyx lilljeborgi Boeck, 1870

SYNONYMY

Anonyx lilljeborgi Boeck, 1870, p. 29; Boeck, 1871, p. 154, pl. IV, fig. 3; Sars, 1891, p. 90, pl. 32, fig. 1; Stebbing, 1894, p. 8; Stebbing, 1906, p. 55; Gurjanova, 1951, p. 223, fig. 88; Gurjanova, 1962, p. 225, fig. 70A (part), 70B (not *A. lilljeborgi lebedi* Gurjanova, 1962, p. 229, fig. 71; nor *A. lilljeborgi* ?; Hurley, 1963, p. 112, fig. 37).

Lakota carinata Holmes, 1908, p. 498, fig. 9; Gurjanova, 1962, p. 302, fig. 100 (as *Lacota c.*)

Lakota carinata (part) — Thorsteinson, 1941, p. 54, pl. 2, fig. 16–17.

Anonyx nugax — Shoemaker, 1930b, fig. 1 (not *A. nugax* Phipps, 1774).

Anonyx nugax (part) — Stephensen, 1923, p. 78; Shoemaker, 1930b, p. 8 (not fig. 1); Stephensen, 1935, p. 64.

Anonyx carinatus — Hurley, 1963, p. 103, fig. 32–34.

DIAGNOSIS OF MATURE FEMALE

Small, interantennal angle of head produced, ventral head margin concave, first peduncular segment of antenna 1 with a convex dorsal profile, upper lip produced into a large rounded lobe, segment 6 of peraeopod 1 narrowed very little distally, dactyl with an accessory tooth, dactyl of peraeopod 2 small, hind edge of peraeopods 3 and 4 with a row of pairs of long setae, segment 2 of peraeopod 7 as long as rest of the limb, hind edge faintly and uniformly serrated, inner edge of the outer ramus of uropod 2 without spines, inner ramus of uropod 2 constricted and bearing a long spine at level of the constriction, inner and outer edges of uropod 3 with setae, lower posterior corner of the second metasome lateral plate with an inconspicuous tooth, posterior projection of the third metasome lateral plate somewhat elongated, slightly upturned, evenly rounded ventrally and not produced at the tip.

DESCRIPTION OF MATURE FEMALE

This is a small species maturing within a size-range of 9–18 mm. The integument is chalky, with weakly developed pebble-grained sculpture.

Head.—Shorter than the first two segments of the mesome combined, interantennal lobe making an acute angle, rounded, lower margin concave. Eye of medium size, red-brown in colour,

expanded only slightly at the bottom, posterior margin almost straight and often half hidden by the whitish integument.

Antenna 1.—Peduncle large, equal in length to the head.

Antenna 2.—With a row of feathery setae on the lower edge and a row of setae on the dorsal edge of the fourth segment of the peduncle. Two groups of long setae and a few feathery setae on the lower edge and a row of setae on the dorsal edge of the fifth segment. Flagellum short with short ventral setae.

Upper lip.—Large, projecting well in front of the epistome as a high lobe, usually evenly rounded, but sometimes a little angular ventrally.

Right mandible.—A single large tooth on the cutting edge. Three spine-teeth and about nine hairy setules in the spine row. Palp, second segment cylindrical and longer than the third, which is hairy on the anterior surface and bears only simple coarse setae.

Left mandible.—Two teeth on the cutting edge.

Maxilla 1.—Outer lobe bearing five short and six long slender spines each with from two to seven accessory teeth. Palp distally expanded, distal margin bearing eight broad, conical, socketed teeth on short stalks, and one small unsocketed tooth on the inner corner.

Peraeopod 1.—Coxal plate expanded anteriorly into a rounded lobe, maximal width shorter than the height below the antero-proximal corner. Segment 6 slightly narrowed distally, equal in length to segment 5, palm perpendicular and defined by two stout spines with accessory hair. Dactyl slightly longer than the palm, with a few setules and an accessory tooth.

Peraeopod 2.—Sixth segment two-thirds of the length of the fifth, palm straight, defined by a single blunt spine, and produced noticeably under the small dactyl which is finely pectinate on the inner margin.

Peraeopods 3 and 4.—Posterior edge of segment 6 with a row of pairs of long setae. Blunt spine at the posterior corner of the sixth segment proportionately large, hooked and in some instances with an accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with usually less than 20 weak serrations, those of the distal half not more crowded or prominent than the proximal ones; maximal length of the segment about equal to or longer than the rest of the limb.

Branchial vesicles.—On peraeopods 2 to 6, transversely pleated into ridges on both sides; on peraeopod 7, unpleated; on peraeopods 5 and 6, with accessory lobes.

Metasome segment 1.—Anterior margin of the lateral plate not setose, produced anteriorly at the anterior corner.

Metasome segment 2.—Lateral plate setose on the anterior, but not on the ventral edge, and produced at the ventral posterior corner into a very small tooth.

Metasome segment 3.—Not carinate dorsally. Lateral plate setose anteriorly and ventrally, projection fairly long, slightly upturned, with an evenly rounded ventral margin and a not very acute tip without ventral concavity.

Urosome segment 1.—Distinctly carinate dorsally and slightly projecting posteriorly.

Uropod 1.—Rami almost equal. Inner ramus with a row of medium-size spines on the inner edge and small spines on the outer surface. Outer ramus with small spines on the outer edge (the distal spine stout, blunt, and ridged and the proximal spines acute) but without spines on the inner edge.

Uropod 2.—Rami almost equal. Inner ramus constricted at the beginning of its distal third, with a long spine (one-half to six-tenths of the distance from it to the end of the ramus) at the constriction, three or four shorter proximal spines, outer surface with one to three short spines. Outer ramus without spines on the inner edge and with a row of short spines on the outer edge, the distal spine being stout, blunt, and ridged.

Uropod 3.—Rami tapering from the anterior third, all four edges nearly straight and bordered with plumose setae. Outer ramus with a second segment of medium length (one-sixth to one-seventh of that of the proximal) and a total length greater than that of the inner ramus, and a few ventral spines. It must be noted here that small mature females from the southern part of the distributional range (such as the Norwegian type-localities, the east coast of the United States, and California) do not usually have setae developed on the four margins of the rami,

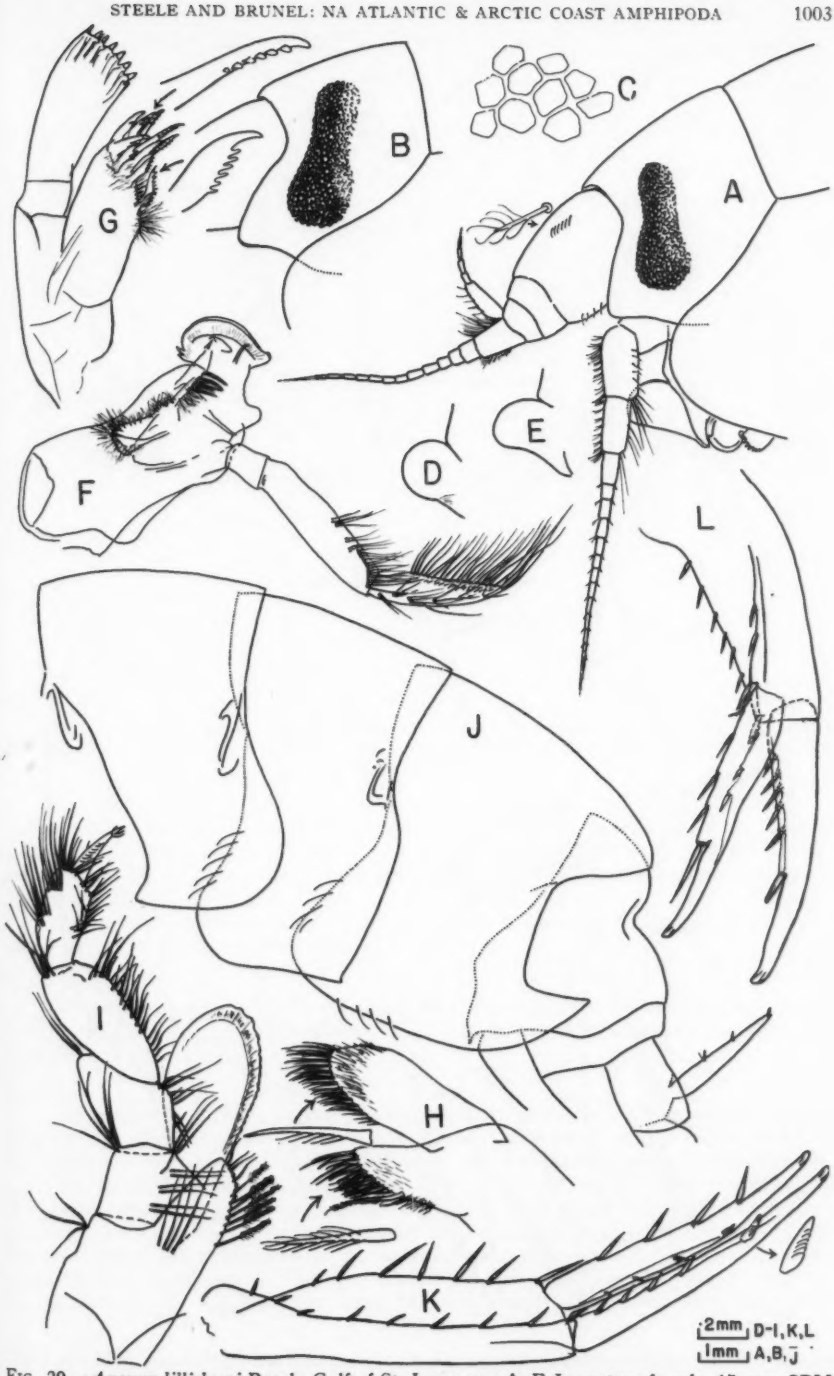

FIG. 29. *Anonyx lilljeborgi* Boeck. Gulf of St. Lawrence. A, F–L, mature female, 17 mm, SBM Sta. PB5. A, anterior; C, sculpturing; F, left mandible; G, maxilla 1; H, maxilla 2; I, maxilliped; J, pleon; K, uropod 1; L, uropod 2; B, head of mature male, 15 mm, SBM Sta. D57; D, upper lip of another mature male, 15 mm, and of an immature female, 15 mm, SBM Sta. D165 (applies to both); E, upper lip of another mature male, 15 mm, SBM Sta. D57.

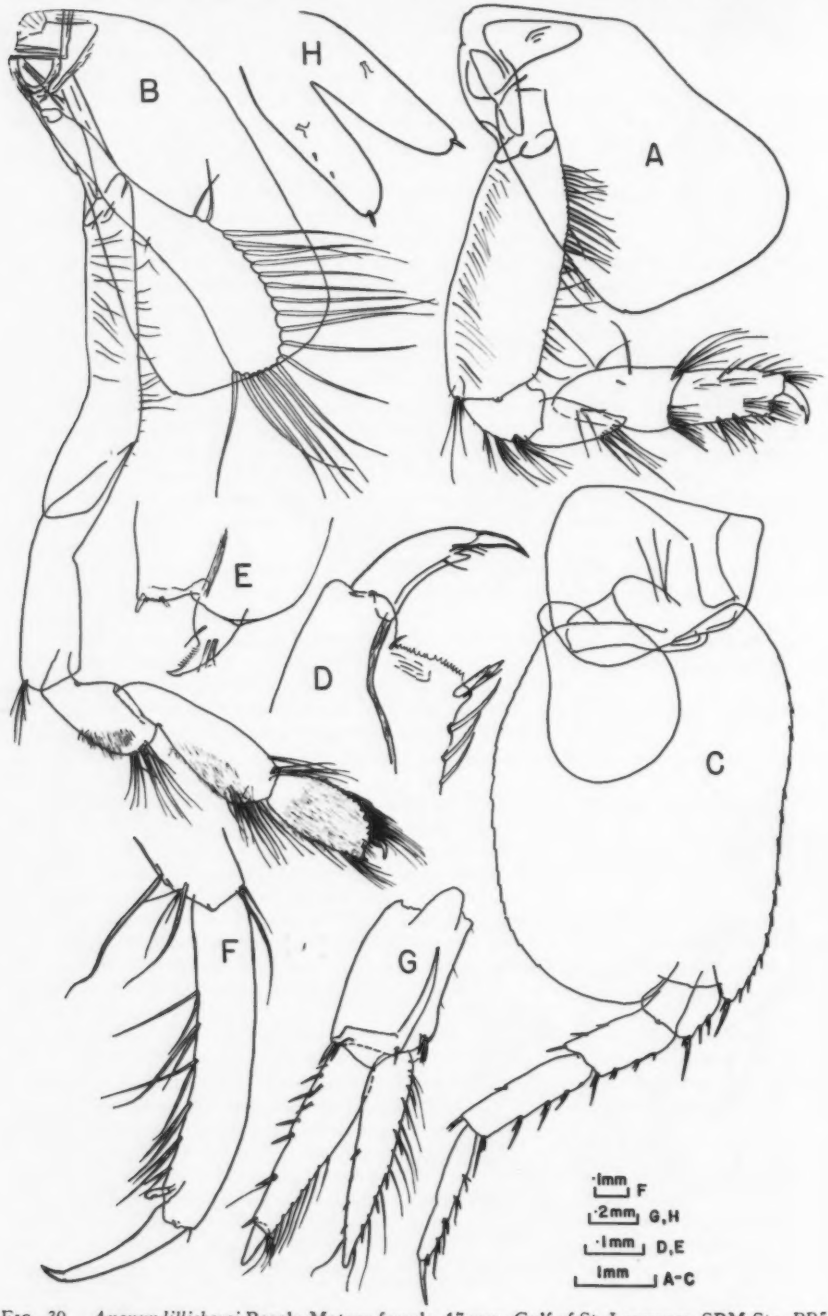

FIG. 30. *Anonyx lilljeborgi* Boeck. Mature female, 17 mm, Gulf of St. Lawrence, SBM Sta. PB5. A, D, peraeopod 1; B, E, peraeopod 2; C, peraeopod 6; F, peraeopod 3; G, uropod 3.

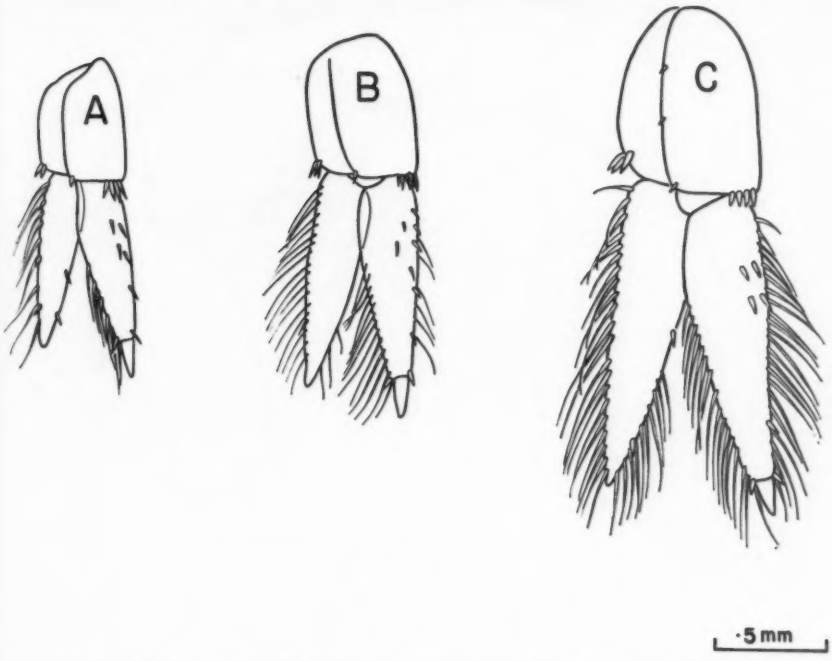

FIG. 31. *Anonyx lilljeborgi* Boeck. Uropod 3. Immature female, 13 mm, Nuvuk Harbour, Hudson Strait. B, immature female, 15 mm, Nuvuk Harbour; C, mature male, 16 mm, Evans Strait, Hudson Bay.

but may have them only on the inner edges (as on Holmes' type-specimen of *Lakota carinata*), or on the inner edges and the outer edge of the inner ramus (as on Boeck's paratype). In this respect they are like intermediate developmental stages of immature individuals from colder localities (Fig. 31).

Telson.—Deeply cleft, each lobe with a single spine in a notch of the apex, and three spines and a pair of setules on its dorsal surface.

MATURE MALE

The mature male is similar to the female but the antennae are elongated and are equipped with calceoli; the eye may be a little larger; and the third uropod has a more extensive armature of plumose setae.

YOUNG

No embryos or hatched young of this species were available for study. The smallest specimens found in the collections were 4–6 mm long. Specimens of this size are very similar to *A. nugax* and *A. pacificus* of the same size, from which they may be distinguished only with difficulty.

The shape of the head is similar to that of young *A. nugax* in that the interantennal lobe is right-angled and the lower margin straight. The upper lip is large, rounded, and extends well in front of the epistome. The spines on the outer lobe of the first maxilla have from two to eight teeth and the second segment of the palp is distally expanded but with only six short conical socketed teeth on short stalks. The sixth segment of peraeopods 3 and 4 has pairs of long setae on the hind margin. As in the adult, segment 2 of peraeopod 7 has a posterior margin which is

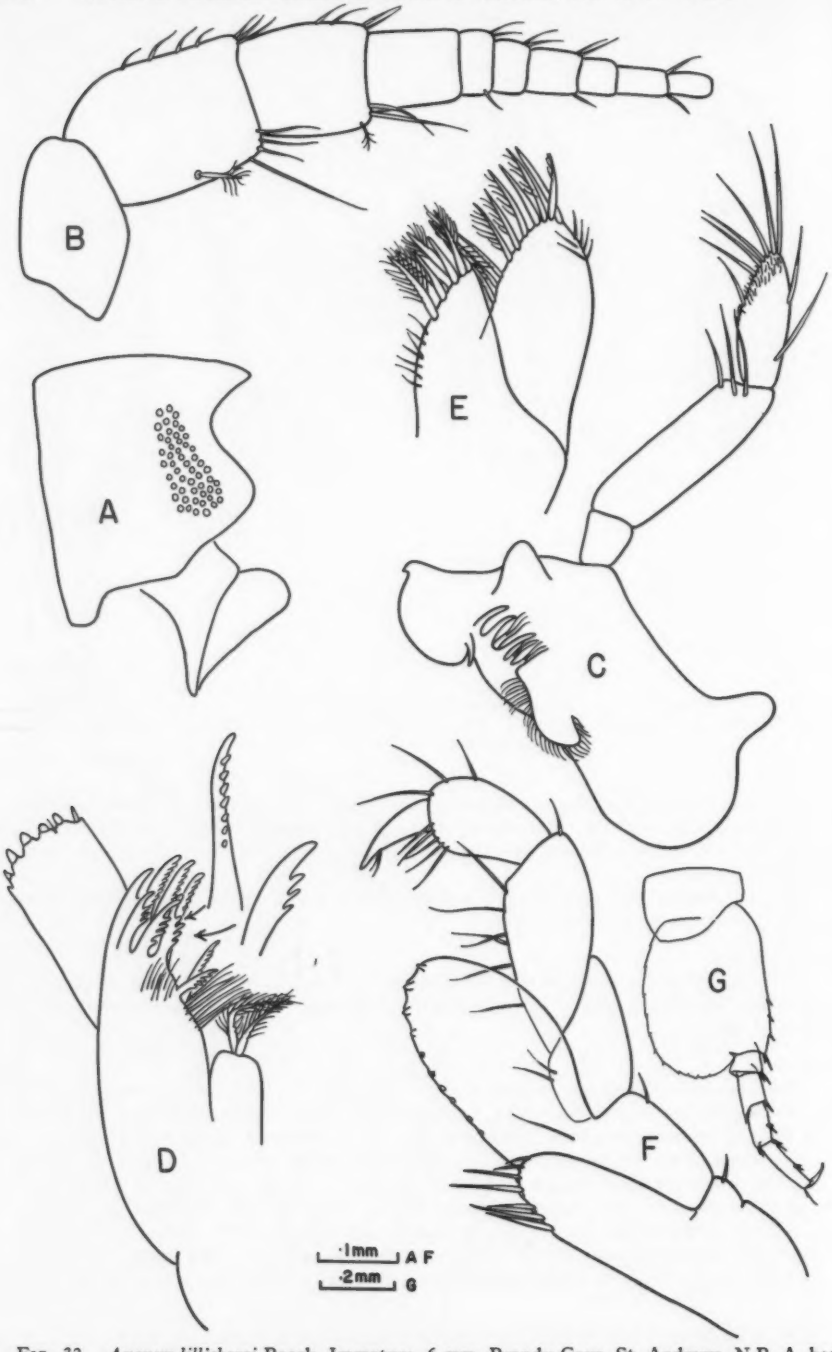

FIG. 32. *Anonyx lilljeborgi* Boeck. Immature, 6 mm, Brandy Cove, St. Andrews, N.B. A, head and upper lip; B, antenna 2; C, right mandible; D, maxilla 1; E, maxilla 2; F, maxilliped; G, peraeopod 7 of immature, 4.5 mm, Gulf of St. Lawrence, SBM Sta. D57.

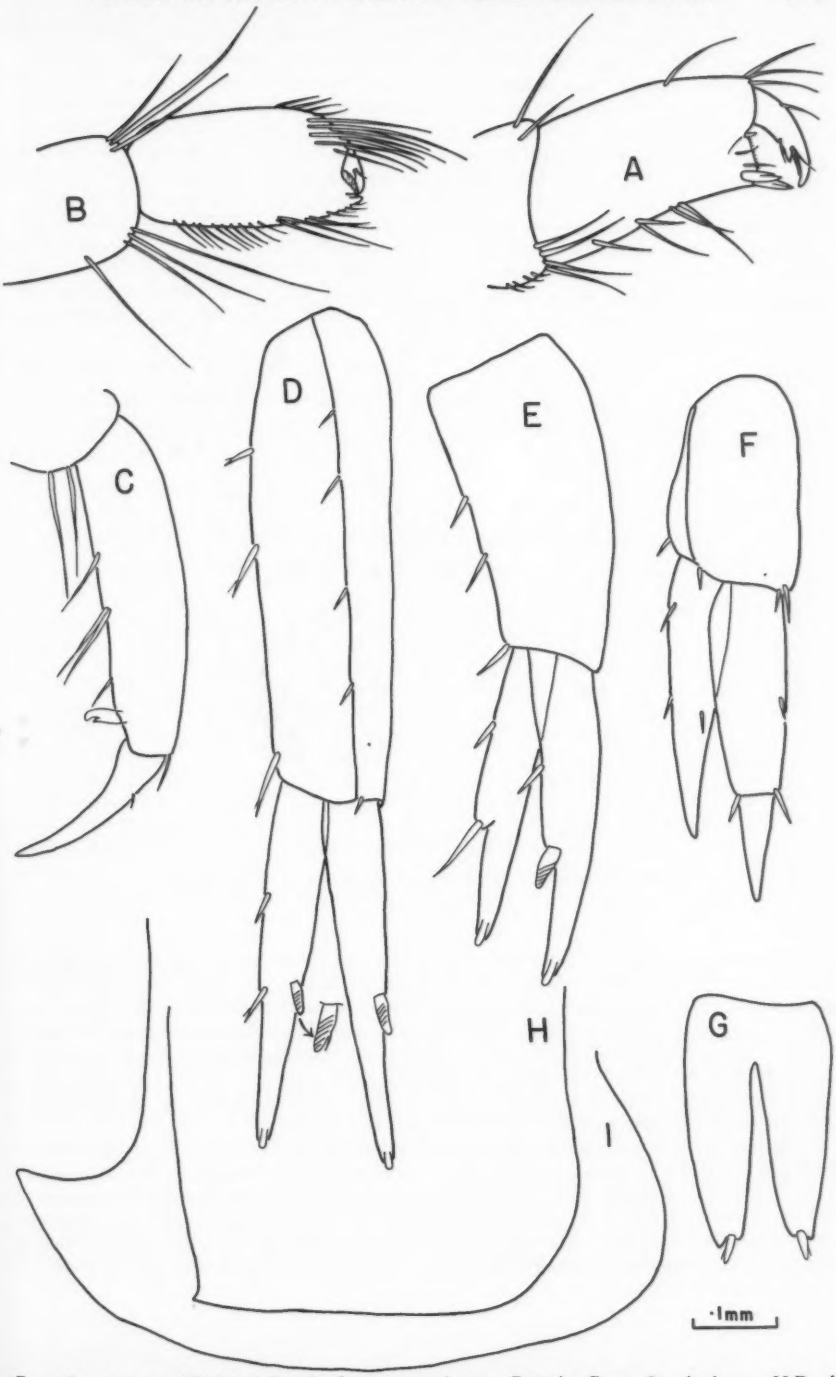

FIG. 33. *Anonyx lilljeborgi* Boeck. Immature, 6 mm, Brandy Cove, St. Andrews, N.B. A, peraeopod 1; B, peraeopod 2; C, peraeopod 3; D, uropod 1; E, uropod 2; F, uropod 3; G, telson; H, lateral plate of second metasome segment; I, lateral plate of third metasome segment.

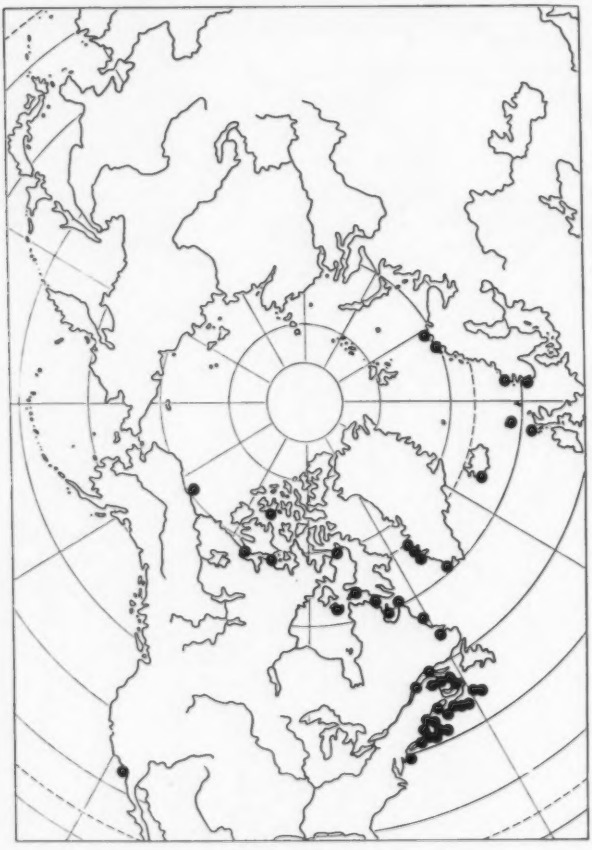

FIG. 34. Distribution of *Anonyx lilljeborgi* Boeck based on examined material.

not distinctly more closely or prominently serrated at its distal than at its proximal half; the segment is also as long as or longer than the distal rest of the limb. The lower portion of the posterior margin of the second metasome lateral plate is almost straight with a very small tooth at the corner, which forms an obtuse or nearly straight angle. The distal spine on the outer margin of each ramus of uropod 1 and of the outer ramus of uropod 2 is ridged. The inner ramus of uropod 2 is constricted just beyond the middle and the spine at the constriction is very long (two-thirds of the distance from its insertion to the end of the ramus). The distal segment of the outer ramus of uropod 3 is longer than half the length of the proximal segment.

As this description indicates, specimens of this size are very similar to *A. pacificus* in most characters, including the structure of uropod 2 which may serve to distinguish them from *A. nugax*. However, the smaller tooth on the lower posterior corner of the second metasome lateral plate, the weak serrations of the hind edge of segment 2 of the seventh peraeopod, and the greater length of the latter segment as compared with the rest of the limb, are distinctive, although these characters must be interpreted with caution. (Both sides of the body must often be examined for a confident conclusion.)

TYPE-SPECIMENS

Holotype: Boeck's holotype presumably came from the Oslo Fjord, the first locality mentioned with his original description (1870). Sars (1891) writes: "the dissections made by Boeck of his type specimen have been preserved in our collection, and from these the detail-figures here given were drawn." An inquiry at the Zoologisk Museum, Universitetet i Oslo revealed (letter of November 12, 1962 from Dr Nils Knaben) that "no material labelled *lilljeborgii* Boeck is to be found at our museum in Oslo." These mounted appendages have been found nowhere else either.

Paratype: one immature male, about 9 mm long, from Haugesund, west coast of Norway (about 59°25′N, 5°16′E), 60–70 fath, 110–128 m, from Boeck's original material; Haugesund is the only other locality mentioned in his paper of 1870. Zoologisk Museum, Universitetet i Bergen, Bergen, Norway, Cat. No. 3032 (pleon segments 3–5 are separated from the rest of the body). This specimen has been kindly lent for study to the junior author by the Bergen Museum, through Dr Johannes Kjennerud.

VARIATION

As in the other species, the size at maturity increases from south to north (Table VIII) and the spines and setae are better developed on the northern specimens.

TABLE VIII. Size (mm) at maturity of *Anonyx lilljeborgi* in different areas.

	Male		Female	
	Maximum size of immature individuals	Size-range of mature individuals	Maximum size of immature individuals	Size-range of mature individuals
Ungava Bay	16	16–17	15	17
Gulf of St. Lawrence and Estuary	15	13–17	16	12–17
Nova Scotia Shelf	15	12–14	13	13–14
Georges Bank and Gulf of Maine	12	13–15	13	9–14
Delaware	–	10–12	–	–

REMARKS

This species was described almost 100 years ago, but until recently most investigators have concluded that it was a young stage of *A. nugax* because of inadequate descriptions and a failure to appreciate the changes in the morphology of these species as they grow. There is a striking resemblance between similar-size specimens in general appearance, in the armature and proportions of the uropods and peraeopods, and yet the adults of *A. nugax*, which are much larger animals, are quite different and easily distinguished. *Anonyx lilljeborgi* possesses distinctive characters in the shape of its head and lateral plates of the metasome, large upper lip, and the plumose setae on the outer edges of the rami of uropod 3. It matures at a much smaller size and

has a different distribution from *A. nugax* so that there is overwhelming evidence for considering it a valid species.

One of Boeck's type-specimens, as well as Danielssen's specimen from Molde (a 10-mm female with non-setiferous oostegites), referred to and presumably used by Sars (1891), have been examined and found to agree in all particulars with the description given above: we have no doubt that all are the same species. Upon examination, the type-specimen of *Lakota carinata* (to be redescribed and illustrated elsewhere) was also determined to be *A. lilljeborgi*, and it is quite evident that the *A. carinata* described and figured by Hurley (1963) (not his *A. lilljeborgi*) is this species.

Shoemaker's (1930b) very accurate drawing of the head, antennae, and upper lip of an "*Anonyx nugax* (Phipps)" obviously represents a mature male of *A. lilljeborgi*. Gurjanova's (1962) drawings (Fig. 70A) of this species apparently indicate a difference in the second uropod between the male and the female: the latter has an unconstricted inner ramus and a distal spine which is not longer than the proximal ones, whereas in the male the ramus is more like that illustrated here (Fig. 29L and 33E) for individuals of both sexes and all sizes from the North Atlantic and Arctic, including Boeck's paratype. We suspect that Gurjanova has mixed appendages of two species in her illustration.

Gurjanova (1962) also describes the new subspecies *A. lilljeborgi lebedi* from the Kuril continental shelf. It is clear from her description and illustrations, and from examination of a specimen from the Beaufort Sea which we have found in the collections of the National Museum of Canada, that a distinct valid species is involved, which is closely related to *A. multiarticulatus* (Pearse), *A. validus* Gurjanova, and *A. laticoxae* Gurjanova.

Distribution

Gurjanova (1962) considers this to be an amphiboreal species found in areas with an Atlantic (Spitzbergen, Franz Joseph Land, and northern Kara Sea) or Pacific influence (Bering, Okhotsk, and Japan seas) but apparently not north of Siberia. However, there does not appear to be any gap in its distribution across North America, even though it has a more southern distribution than *A. nugax*, is most abundant from the Gulf of St. Lawrence southward, and has been found as far south as Delaware and California (Hurley, 1963). It is found generally on sandy substrates from the intertidal region down to a depth of several hundred metres, including the very cold (about −1 to +1 C the year round) intermediate water layer of the Gulf of St. Lawrence.

Anonyx ochoticus Gurjanova, 1962

Synonymy

?Anonyx affinis Ohlin, 1895, p. 24, fig. 15–18; Stebbing, 1906, p. 55 (not Gurjanova, 1951, p. 224, fig. 89, nor Gurjanova, 1962, p. 285, fig. 93A–B).

Lakota carinata (part) — Thorsteinson, 1941, p. 54, pl. 2, fig. 16–17.

DIAGNOSIS OF MATURE FEMALE

Small, upper lip projecting only slightly in front of the epistome, segment 6 of the first peraeopod narrowed only slightly distally, dactyl of peraeopod 1 with an accessory tooth, dactyl of peraeopod 2 small, hind edge of segment 6 of peraeopods 3 and 4 with a double row of long setae, segment 2 of peraeopod 7 a little shorter than rest of the limb, hind edge with uniformly faint and well-spaced serrations, inner ramus of uropod 2 completely constricted and bearing a long spine at the constriction, first segment of the urosome markedly keeled and overhanging the second segment posteriorly, second metasome lateral plate without an obvious tooth on the postero-ventral corner.

DESCRIPTION OF MATURE FEMALE

This is one of the smallest known species of *Anonyx*, maturing at a size of 9–11 mm. The body is laterally compressed, especially in the third metasome segment and the urosome. The only noticeable sculpturing consists of small pits on the metasome and urosome.

Head.—Shorter than the combined length of the first two segments of the mesosome. Interantennal lobe making a rounded right angle, lower margin nearly straight. Eye narrow, moderately expanded at the bottom and not occupying much of the interantennal lobe, posterior margin straight, red-brown to black on preserved specimens.

Antenna 1.—Peduncle shorter than the head, first segment stout, as high as it is long, dorsal profile convex. Flagellum short.

Antenna 2.—Feathery setae in a row on the lower edge of the fourth and scattered on the lower edge of the fifth segment of the peduncle. Short setae in a scattered row on the dorsal edge of each segment. Flagellum short, with very short ventral setae.

Upper lip.—Projecting only slightly in front of the epistome as an evenly rounded lobe, sometimes ventrally angular.

Right mandible.—With a single prominent tooth on the cutting edge. Three spine-teeth in the spine row, and four hairy setules, the distal one bush-like. Palp, second segment cylindrical and one and a half times as long as the third, which is hairy on the anterior surface.

Left mandible.—Two large and one small teeth on the cutting edge.

Maxilla 1.—Outer lobe truncate, and bearing five short spines each equipped with from two to five teeth and six long spines each with two to eight teeth. Palp distally expanded and bearing eight broad conical teeth in sockets but not on stalks, and one small unsocketed tooth on the inner corner.

Peraeopod 1.—Coxal plate expanded anteriorly and rounded, maximal width shorter than the height below the antero-proximal corner. Segment 6 longer than segment 5, palm perpendicular, and defined by two stout spines with accessory hair, the inner spine only one-half the length of the outer. Dactyl longer than the palm and bearing a small accessory tooth and a few setae on the inner edge.

Peraeopod 2.—Segment 6 about one-half of the length of segment 5, covered distally and ventrally by long setae with a forked tip and a pectinate medial margin. Palm straight or slightly convex, minutely denticulate, and produced under the medium-size pectinate finger to form a small imperfect chela.

Peraeopods 3 and 4.—Posterior edge of segment 6 with a row of pairs of long setae; blunt spine on the posterior corner of the sixth segment proportionately large, hooked, and with a small accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with less than 20 (usually not more than 15) serrations, neither more prominent nor much more crowded in the distal than in the proximal half of the segment; maximal length of the segment only a little shorter than the distal rest of the limb.

Branchial vesicles.—On peraeopods 2–7 unfolded; on peraeopods 5 and 6 with an accessory lobe.

Metasome segment 1.—Lateral plate without setae on the anterior edge and produced at the anterior lower corner.

Metasome segment 2.—Lateral plate setose on the anterior and ventral edges; lower posterior corner making a blunt right or slightly obtuse angle, and provided with one, two, or three very minute teeth (which are very difficult to see even on perfect specimens).

Metasome segment 3.—Dorsally carinate. Lateral plate setose ventrally and anteriorly, posterior projection short with an evenly rounded but strongly upturned posterior margin, and a moderately acute tip without ventral concavity.

Urosome segment 1.—Carinate dorsally and strongly projecting posteriorly to overhang the second segment, the median carina beginning anteriorly at a rather distinct point, between two shorter but more acute lateral and oblique dorsal keels, and ending posteriorly in a heeled lobe which often makes a rounded angle with the dorsal edge.

Uropod 1.—Rami almost equal. Inner ramus with four long spines on its inner margin, and one ridged and blunt distal spine and an acute proximal spine on its outer margin. Outer ramus with two small spines on the inner and three small and two larger ridged and blunt spines on the outer edge.

Uropod 2.—Rami almost equal. Inner ramus completely constricted beyond the middle (one-third to two-fifths the distance to the end of the ramus) and bearing a long stout spine at the point of the constriction. This spine is four to five times the length of the single proximal spine on the inner edge (there are no spines on the outer edge) and extends well beyond half the distance from its insertion to the end of the ramus. Outer ramus with a row of medium-size spines on the outer margin (the two distal ones being stouter, ridged, and blunt), but none on the inner margin.

Uropod 3.—Rami narrow, almost equal in length, edges nearly straight and tapering from their proximal third or farther toward their base. Outer ramus with the second segment one-third of the length of the proximal segment. Edges of both rami with spines but without setae.

Telson.—Cleft to two-thirds of its length and bearing a single spine in each apical notch and two to three small spines and a pair of setae on the dorsal surface of each lobe.

The spines of the uropods and of the telson have an accessory hair.

Mature Male

The mature male is similar to the female except for the antennae which are larger, more setose, and composed of more and longer segments bearing calceoli, the second uropod which has more spines and the third uropod which is larger and bears plumose setae on the inner margin of each ramus. The largest males also have a slightly larger eye and a slightly concave lower margin of the head.

Young

One female with hatched young (2.3–2.4 mm) was collected in Conception Bay, Newfoundland. Young specimens of this size lack the carina on the first urosome segment and are similar to the newly hatched young of *A! nugax* and *A. sarsi*. However, the lateral plate of the second metasome segment is rounded posteriorly in *A. ochoticus* whereas in *A. nugax* and *A. sarsi* it is angular.

Specimens 5–6 mm long, although strongly resembling the previously described species in the structure of the head, mouthparts, antennae, and peraeopods, differ from them in the shape and lack of a tooth on the second metasome lateral plate, in the constriction and long spine of uropod 2 and in the carina of the first urosome segment. These characters are quite distinctive even at this size in the present species.

Type-Specimens

We have been unable to discover whether type-specimens of *Anonyx ochoticus* have been designated, or to compare our material with North Pacific specimens identified by the original describer. Three localities with depths of 29–263 m in the Sea of Okhotsk are given for this species by Gurjanova (1962), so that we do not know the type-locality more exactly.

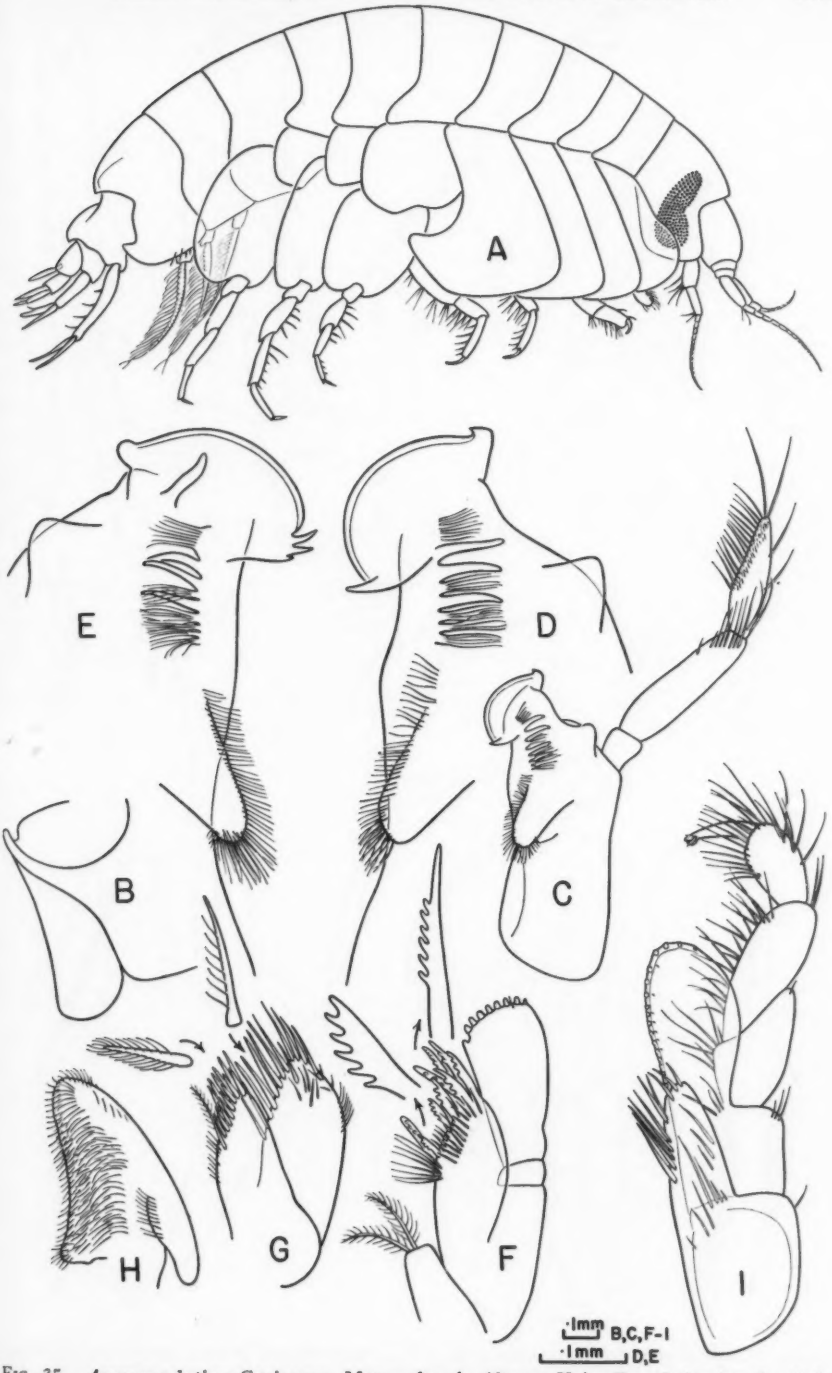

FIG. 35. *Anonyx ochoticus* Gurjanova. Mature female, 10 mm, Unity Bay, Labrador. A, whole animal; B, upper lip; C, D, right mandible; E, left mandible; F, maxilla 1; G, maxilla 2; H, lower lip; I, maxilliped.

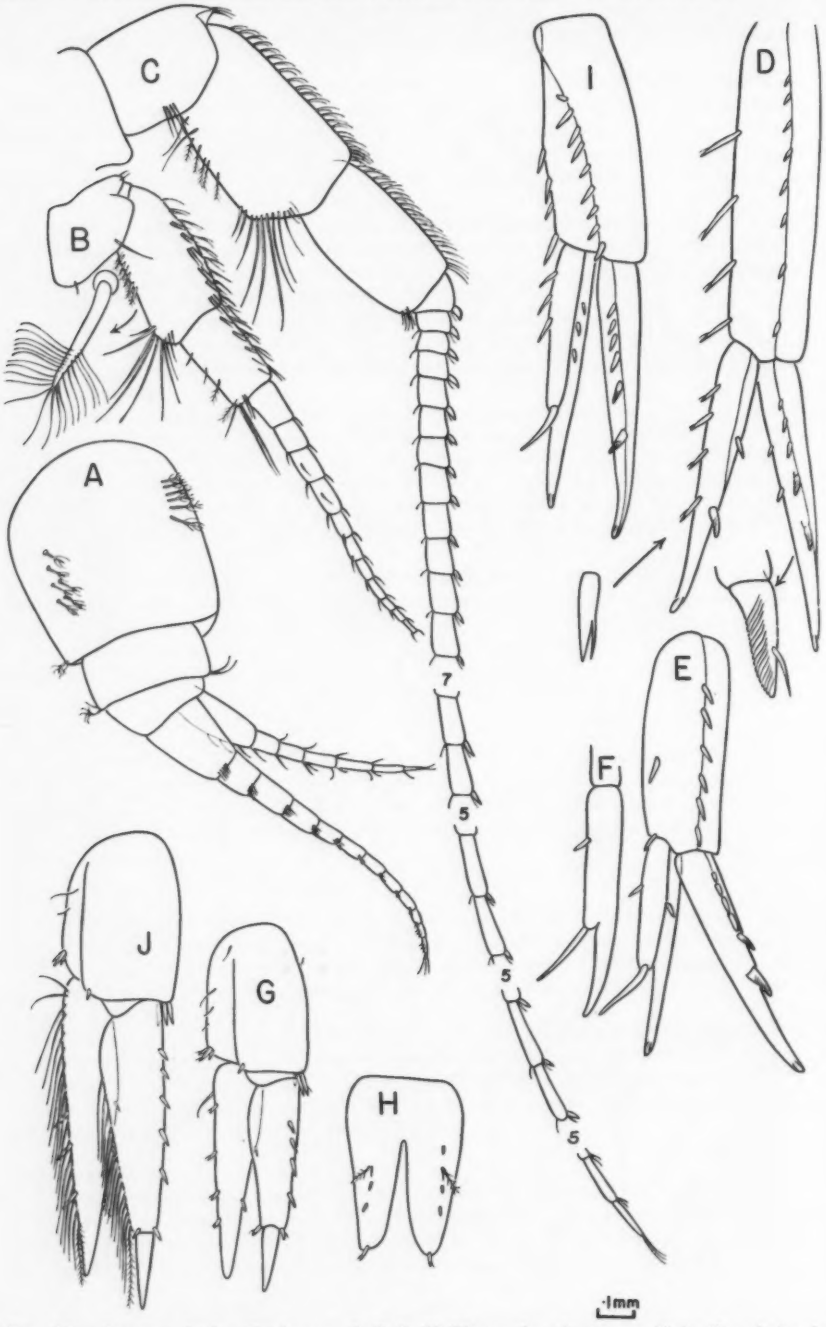

FIG. 36. *Anonyx ochoticus* Gurjanova. A, B, D–H. Mature female, 10 mm, Unity Bay, Labrador. A, antenna 1; B, antenna 2; D, uropod 1; E, uropod 2; F, lateral view of uropod 2; G, uropod 3; H, telson; C, I, J, mature male, 11 mm, Bay of Islands, Newfoundland; C, antenna 2; I, uropod 2, J, uropod 3.

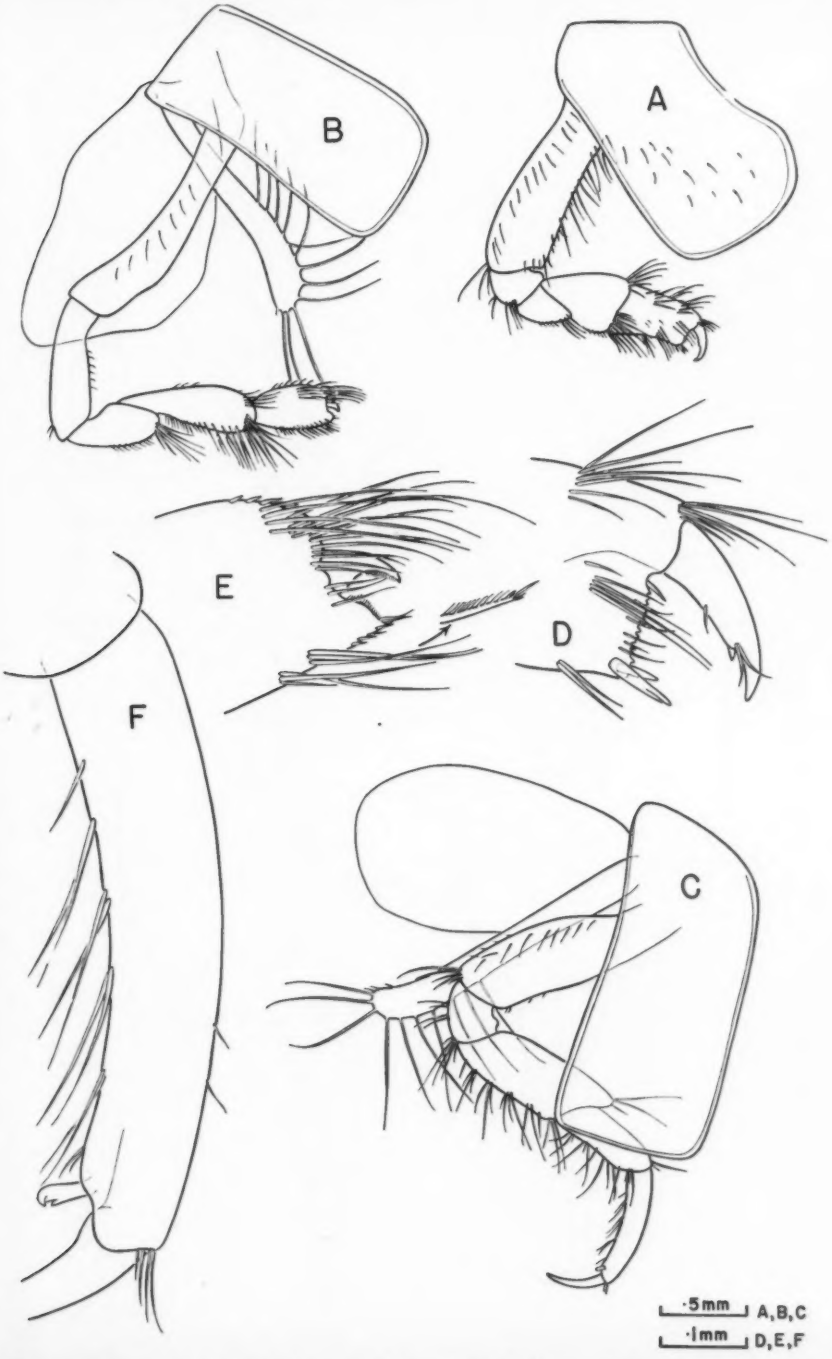

FIG. 37. *Anonyx ochoticus* Gurjanova. Mature female, 10 mm, Unity Bay, Labrador. A, peraeopod 1; B, peraeopod 2; C, peraeopod 3; D, peraeopod 1; E, peraeopod 2; F, peraeopod 3.

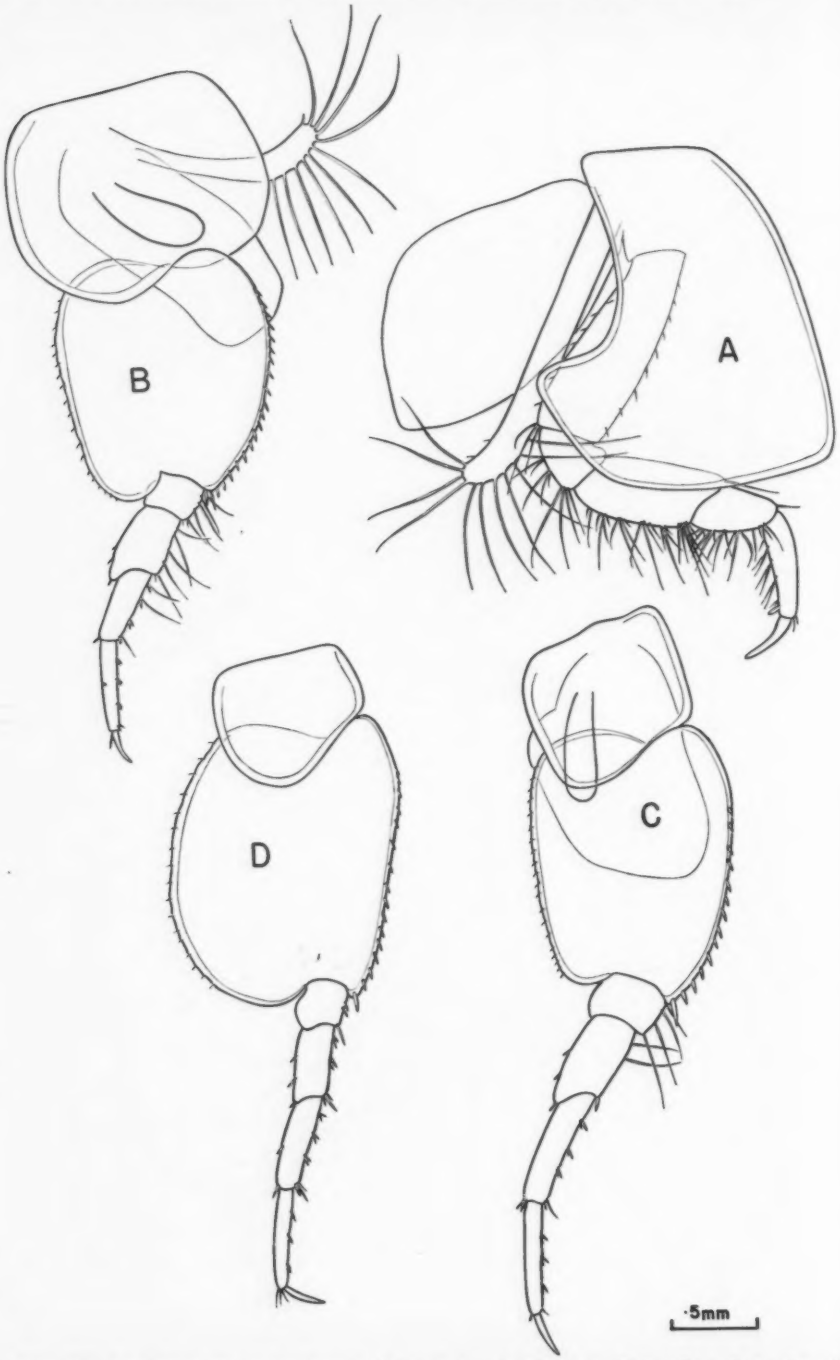

FIG. 38. *Anonyx ochoticus* Gurjanova. Mature female, 10 mm, Unity Bay, Labrador. A, peraeopod 4; B, peraeopod 5; C, peraeopod 6; D, peraeopod 7.

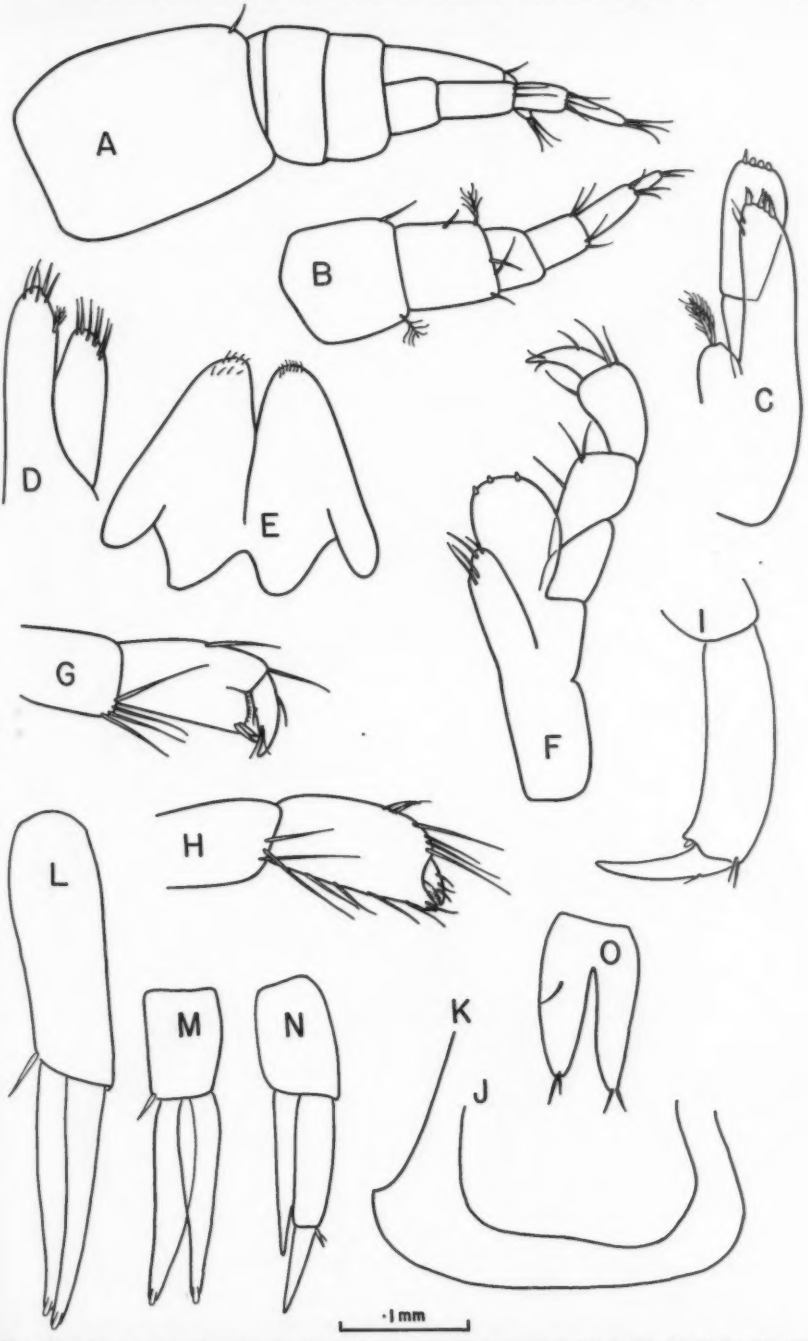

FIG. 39. *Anonyx ochoticus* Gurjanova. Immature, 2.3 mm, from brood pouch of female from Conception Bay, Newfoundland. A, antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, lower lip; F, maxilliped; G, peraeopod 1; H, peraeopod 2; I, peraeopod 3; J, lateral plate of second metasome segment; K, lateral plate of third metasome segment; L, uropod 1; M, uropod 2; N, uropod 3; O, telson.

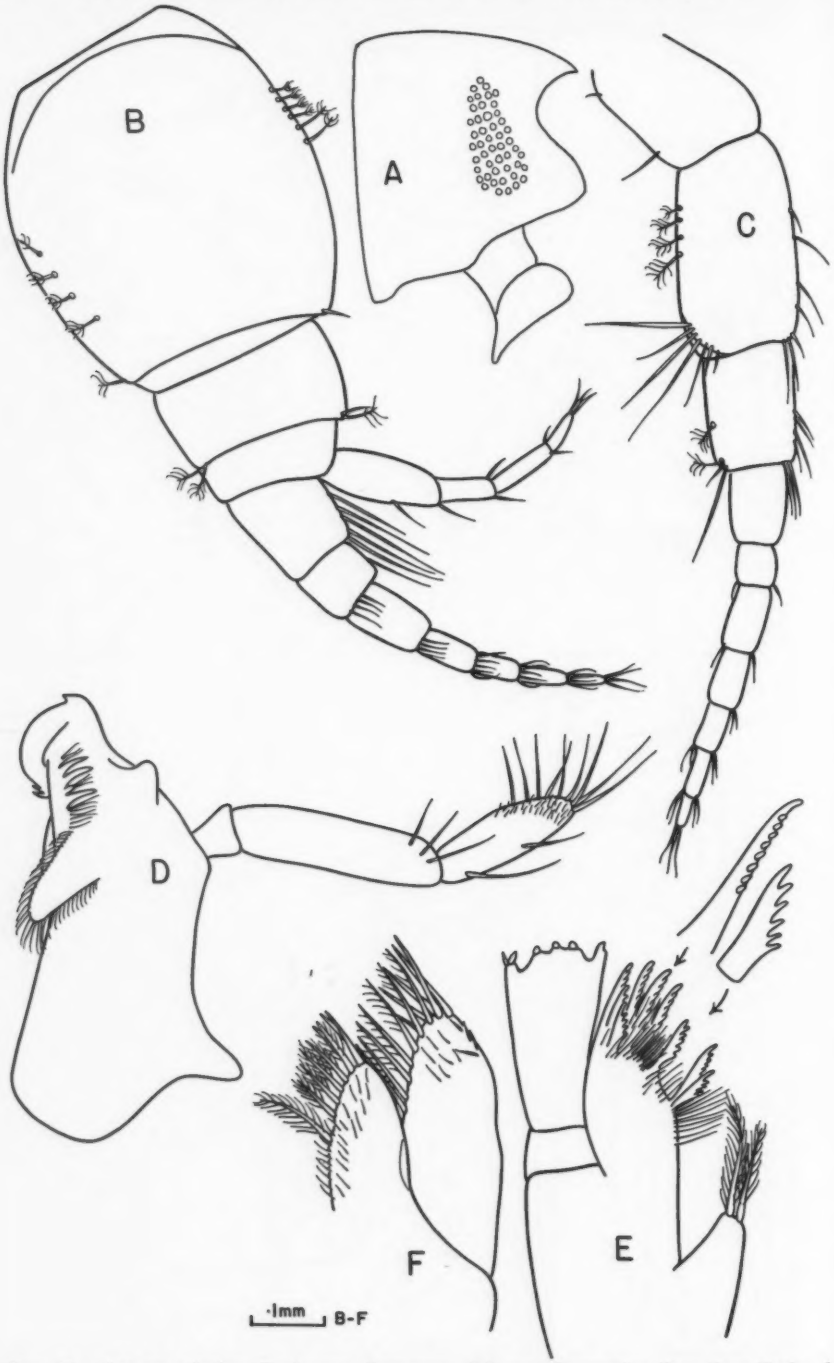

FIG. 40. *Anonyx ochoticus* Gurjanova. Immature, 5.5 mm, Frustration Bay, Foxe Basin. A, head and upper lip; B, antenna 1; C, antenna 2; D, right mandible; E, maxilla 1; F, maxilla 2.

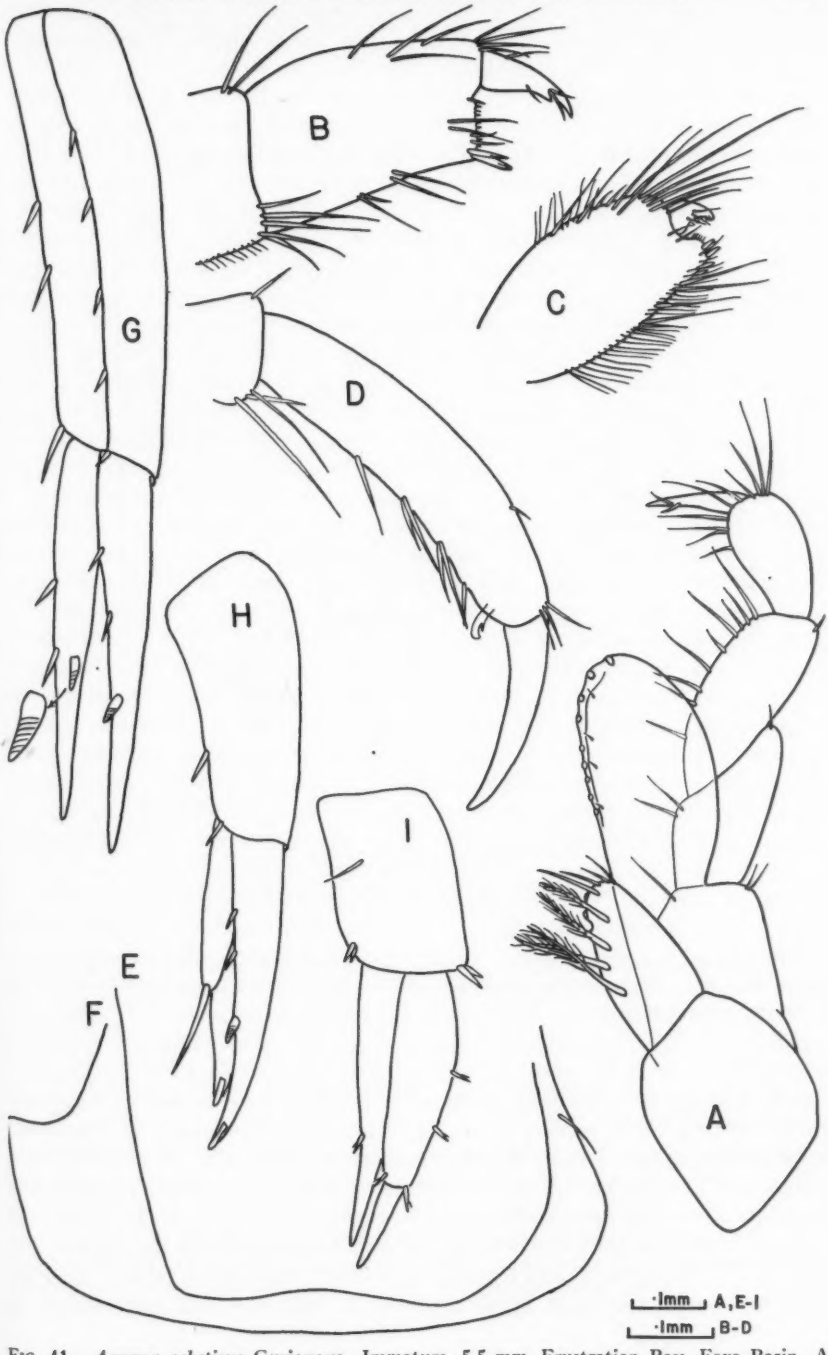

FIG. 41. *Anonyx ochoticus* Gurjanova. Immature, 5.5 mm, Frustration Bay, Foxe Basin. A, maxilliped; B, peraeopod 1; C, peraeopod 2; D, peraeopod 3; E, lateral plate of second metasome segment; F, lateral plate of third metasome segment; G, uropod 1; H, uropod 2; I, uropod 3.

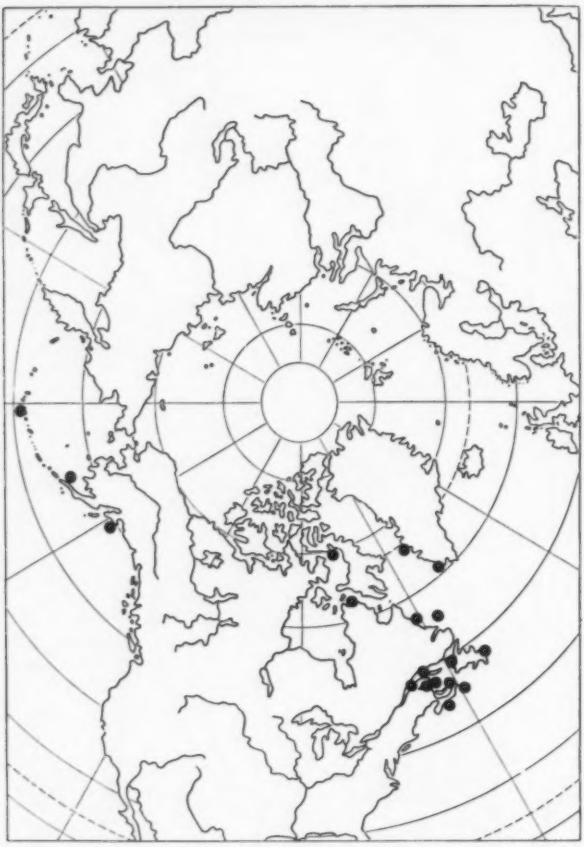

FIG. 42. Distribution of *Anonyx ochoticus* Gurjanova based on examined material.

An intensive search for the type-specimens of *A. affinis*, another possible name for the present species, has failed to discover them at the British, Stockholm, Lund University, and Copenhagen University museums.

REMARKS

At first we identified specimens of this species as *Anonyx affinis*, as described by Ohlin (1895a), largely on the basis of their small size and occurrence in collections taken close to the type-locality in Baffin Bay. A more detailed comparison has disclosed that our specimens differ from *affinis* in numerous characteristics: they are smaller, the first segment of the peduncle of antenna 1 is higher and dorsally less convex, uropod 2 is constricted completely and has a much longer spine, and uropod 3 has fewer setae and a relatively longer inner ramus. On the other hand, considering that all eight Atlantic species

of *Anonyx* have a faint dorsal keel on urosome segment 1, one may reason that Ohlin must have found that of *A. affinis* rather conspicuous (he says "fairly clear keel") to call attention to it. Conversely, when so many previous workers, including even Sars (whose 1891–95 "Account" Ohlin cites), had failed to note the constriction and spine of uropod 2 in *Anonyx*, one surmises that in making his poor drawings, Ohlin's attention was not drawn to this structure. Finally, the size of 13 mm for a mature female specimen of *A. affinis*, at the latitude of Baffin Bay, can only be that of either *A. ochoticus*, *A. compactus*, or a still undiscovered species, according to our present data on sizes of the different species at maturity. A more detailed comparison is not possible from the published description and meagre illustrations and our failure to turn up the type-specimen(s), or any others that could be identified as *A. affinis*, force us to leave this name in its doubtful status. We do not agree with Gurjanova's (1962) use of this name for another North Pacific species which has few diagnostic characters of Ohlin's description, and which we have been unable to discover in waters much closer to the type-locality.

In our opinion there is justification for considering our specimens as distinct from *A. affinis*. On the other hand, Gurjanova (1962) has published the description of a new species (*A. ochoticus*) from the Sea of Okhotsk which apparently is the same as ours. They resemble each other in all essential features, including the dorsal keel on urosome segment 1 and the long spine on the inner ramus of uropod 2, but the specimens described by Gurjanova also show a few minor differences from ours: they are slightly larger (12 mm), the interantennal lobe of the head is more pointed, the upper lip projects more, the first peduncular segment of antenna 1 lacks a keel, and the gills of peraeopod 2 are described as being slightly pleated, those of peraeopod 7 as having an accessory lobe, and the illustrated shape of the dorsal keel of urosome segment 1 is rather different. However, most of these are quantitative minor differences that may be due to size, to geographic variation, to differences in interpretation, or to inaccuracies in the original drawing. (For instance, we are convinced that the outer plates of the maxillipeds are rounded and bordered by minute nodular teeth, as they are in all our *Anonyx* specimens, and not distally angular and coarsely denticulate as represented on Gurjanova's (1962) fig. 93B.) The statements on the presence of an accessory lobe on the last branchial vesicles or the absence of a keel on the first peduncular segment of antenna 1, and on the absence from the third urosome segment of the lateral flaps extending back on each side of the telson, may likewise be in error since these characters are not found in any of the other species of the genus or in our specimens of this species.

Stimpson (1853) has described *Anonyx exiguus*, without giving illustrations, as follows:

> "Minute, compressed, but rounded on the back; last three thoracic segments nearly equalling the first four in extent. Epimera of the first four pairs equalling in height that of the segments which bear them. Abdomen with its third segment tumid posteriorly, and curving downwards to the fourth, thus forming a sinus, which appears deeper from a blunt projection on

the middle of the fifth segment. Head small, with the eyes bright red, or vermillon in color. Superior antennae short and thick, about half the length of the very slender inferior ones, which reach the fourth thoracic segment. Legs slender, in structure nearly the same as in the above species (i.e. *A. pallidus*). The posterior five pairs terminate in long slender fingers. Basal joints of the posterior three pairs very broadly expanded, and deeply serrated along their posterior edges. Caudal stylets as in *A. politus*. Color yellowish. Length, 0.2 inch. Dredged on sandy bottoms in 8–15 fathoms, east of the Passage, and off Cheney's Head."

Stimpson sent a specimen to Bate, who later (1862) gave a drawing of it and endorsed the species. Stebbing (1906) considered the species as doubtful, and it was forgotten from then on. There is a suggestion from Bate's drawing, showing an acute projection to the third lateral plate of the metasome and a strong dorsal keel on urosome segment 1 (not the fifth of the abdomen, as written by Stimpson, probably by mistake) and from the small size (about 5 mm) that *A. exiguus* might have been the same as the species described here as *A. ochoticus*. However, the metasome projection is much too prominent, since *ochoticus* has the least prominent projection, and the bright red eyes do not match in color with those of *ochoticus*. The generic identity of *exiguus* therefore remains uncertain, but is probably not *Anonyx*.

Distribution

Anonyx ochoticus is now known from the Sea of Okhotsk eastward to western Greenland and appears to be another species of Pacific origin that has spread eastward across northern North America. It has been collected at depths of 15–314 m, apparently chiefly in very cold water, but has not been found frequently, probably because of its small size.

Anonyx debruyni Hoek, 1882

Synonymy

Anonyx debruynii Hoek, 1882, p. 44, pl. III, fig. 30–30x.

Chironesimus debruynii — Sars, 1891, p. 109, pl. 37, fig. 2; Stebbing, 1894, p. 13; Stebbing, 1906, p. 72; Stappers, 1911, p. 18 (part) (not pl. 1, fig. 6–8); Stephensen, 1935, p. 90; Gurjanova, 1951, p. 262, fig. 132.

Anonyx debruyni debruyni — Gurjanova, 1962, p. 255, fig. 83A–83B (part) (not *A. debruyni orientalis* Gurjanova, 1962, p. 260, fig. 84).

Diagnosis of Mature Female

Medium-size, cephalic interantennal angle acute and rounded, lower margin markedly concave, upper lip distally angular and markedly produced in front of the epistome, sixth segment of peraeopod 1 much narrowed distally, palm oblique, dactyl with a small accessory tooth, segment 6 of peraeopod 2 expanded distally, palm very long and concave, dactyl very large, hind edge of segment 6 of peraeopods 3 and 4 with a row of pairs of long setae and a few unpaired slender spines, segment 2 of peraeopod 7 coarsely but uniformly serrated on hind edge, as long as rest of the limb, inner ramus of uropod 2 constricted well beyond the middle and bearing a long spine at the level of the constriction, second metasome lateral plate without tooth in the postero-ventral corner, posterior projection of the third metasome lateral plate long, ventrally concave, and produced into an acute tip.

Description of Mature Female

This species matures when 14–21 mm long. The integument lacks sculpturing but bears many pit-like depressions.

Head.—Shorter than the first two segment of the mesosome. Interantennal lobe acutely angled, rounded, lower margin concave. Eye of medium size, narrow, pear-shaped, not occupying most of the interantennal lobe, posterior margin concave, red-brown to black in colour.

Antenna 1.—Peduncle equal in length to the head; first segment a little longer than high, dorsal profile nearly straight. Flagellum short.

Antenna 2.—Fourth and fifth segments of the peduncle with dorsal rows of short setae, fourth with a ventral row of feathery setae, fifth with three groups of long setae on the ventral edge. Flagellum short, with short ventral setae.

Upper lip.—Large, projecting well beyond the epistome as a tapering lobe, which is sometimes rounded, sometimes distinctly angular ventrally.

Right mandible.—With a single rounded tooth on the cutting edge. Three spine-teeth and five to six smaller hairy setules in the spine row. Palp, second segment cylindrical and longer than the third, which is hairy on the anterior surface.

Left mandible.—Similar to the right mandible.

Maxilla 1.—Outer lobe bearing five small broad spines and six long spines each with from one to nine accessory teeth. Palp distally expanded, with 9–10 broad conical teeth without stalks and one small unsocketed tooth in the inner corner.

Peraeopod 1.—Coxal plate not expanded anteriorly, but with a concave anterior edge and rounded antero-distal lobe, maximal width much shorter (1:1.5) than the height below the antero-proximal corner. Segment 6 shorter than segment 5, narrowed distally, palm oblique, short, bordered partly with crowded slender acute denticles and partly with more widely spaced and coarser blunt tubercles, and defined by two to three stout spines each of which has a strong accessory hair, three to five more of these spines occurring in continuous sequence on the distal hind edge of the segment.

Peraeopod 2.—Segment 6 almost equal in length to segment 5, greatly expanded distally, covered on its anterior and posterior margins by long setae with a forked tip and a pectinate medial margin. Palm long, concave, and armed with several series of small rounded denticles and setae. Dactyl very large and minutely setose (or coarsely pectinate) on its inner margin.

Peraeopods 3 and 4.—Posterior margin of the sixth segment bearing a row of pairs of setae, and several spines typically unpaired with the setae; the blunt spine on the posterior corner of the sixth segment medium-size, strongly hooked, and with a small accessory tooth.

Peraeopod 7.—Segment 2, posterior margin with about 20 or fewer medium-size serrations, neither much more prominent nor much more crowded in the distal than in the proximal half of the segment; maximal length of the segment about as long as (sometimes a little longer than) the rest of the limb.

Branchial vesicles.—On peraeopods 2–6 weakly pleated into transverse ridges; on peraeopod 7, unpleated; on peraeopods 5 and 6, with an accessory lobe.

Metasome segment 1.—Anterior edge of the lateral plate sparsely setose, produced anteriorly at the lower corner.

Metasome segment 2.—Lateral plate without setae, lower posterior corner making an obtuse angle, without a tooth.

Metasome segment 3.—Not carinate dorsally. Lateral plate setose ventrally, posterior projection long and narrow, upturned, with a slightly concave posterior margin, and an acute tip.

Urosome segment 1.—Slightly carinate dorsally and slightly projecting posteriorly.

Uropod 1.—Rami almost equal. Inner ramus with medium-size spines on the margins. Outer ramus with small spines.

Uropod 2.—Rami almost equal. Inner ramus constricted close to the beginning of its distal third and bearing a long spine at the level of the constriction. This spine is three times as long as the short and relatively numerous proximal spines on the inner margin, and more than one-half as long as the distance from its insertion to the end of the ramus. Outer ramus with a row of medium-size spines on the outer margin, but only two small spines on the inner margin, one of which is in the distal third of the ramus.

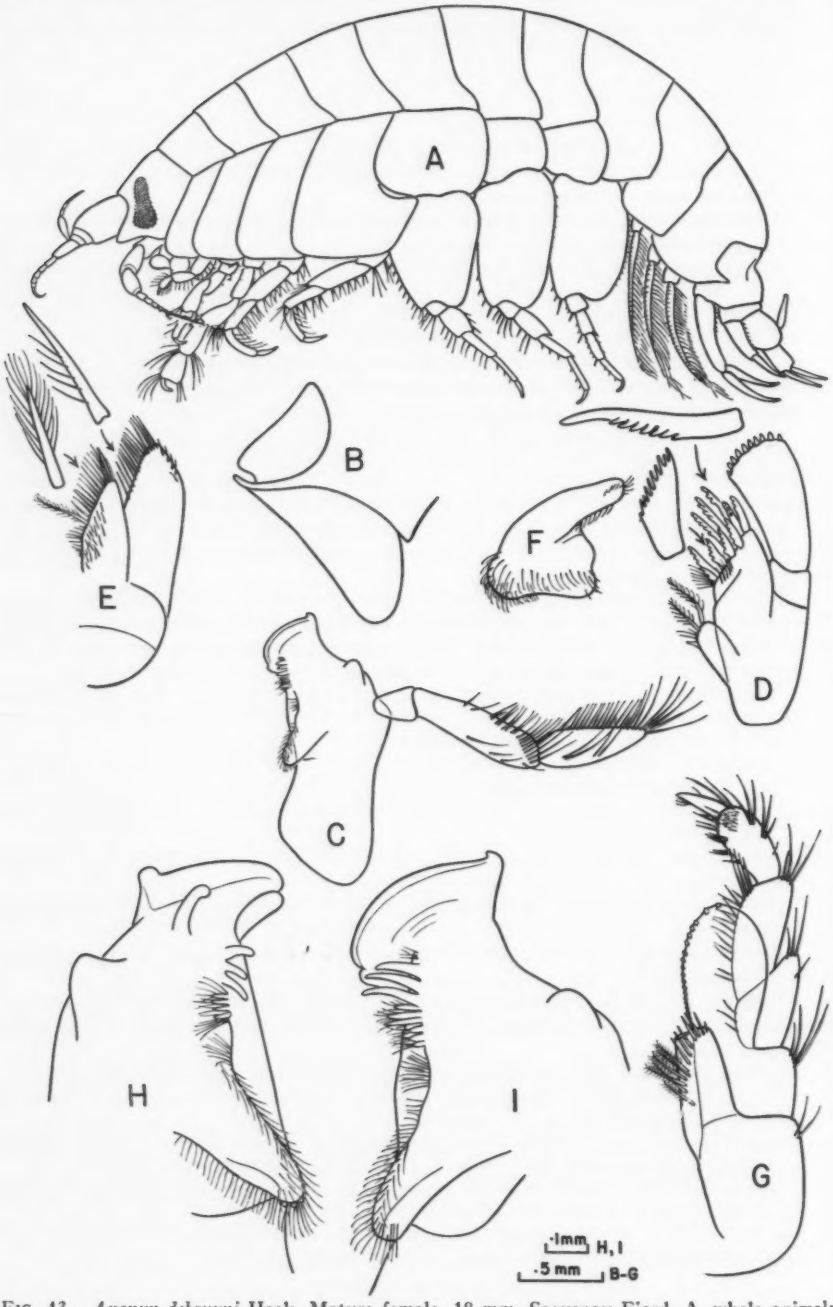

FIG. 43. *Anonyx debruyni* Hoek. Mature female, 18 mm, Saguenay Fjord. A, whole animal; B, upper lip; C, I, right mandible; D, maxilla 1; E, maxilla 2; F, lower lip; G, maxilliped; H, left mandible.

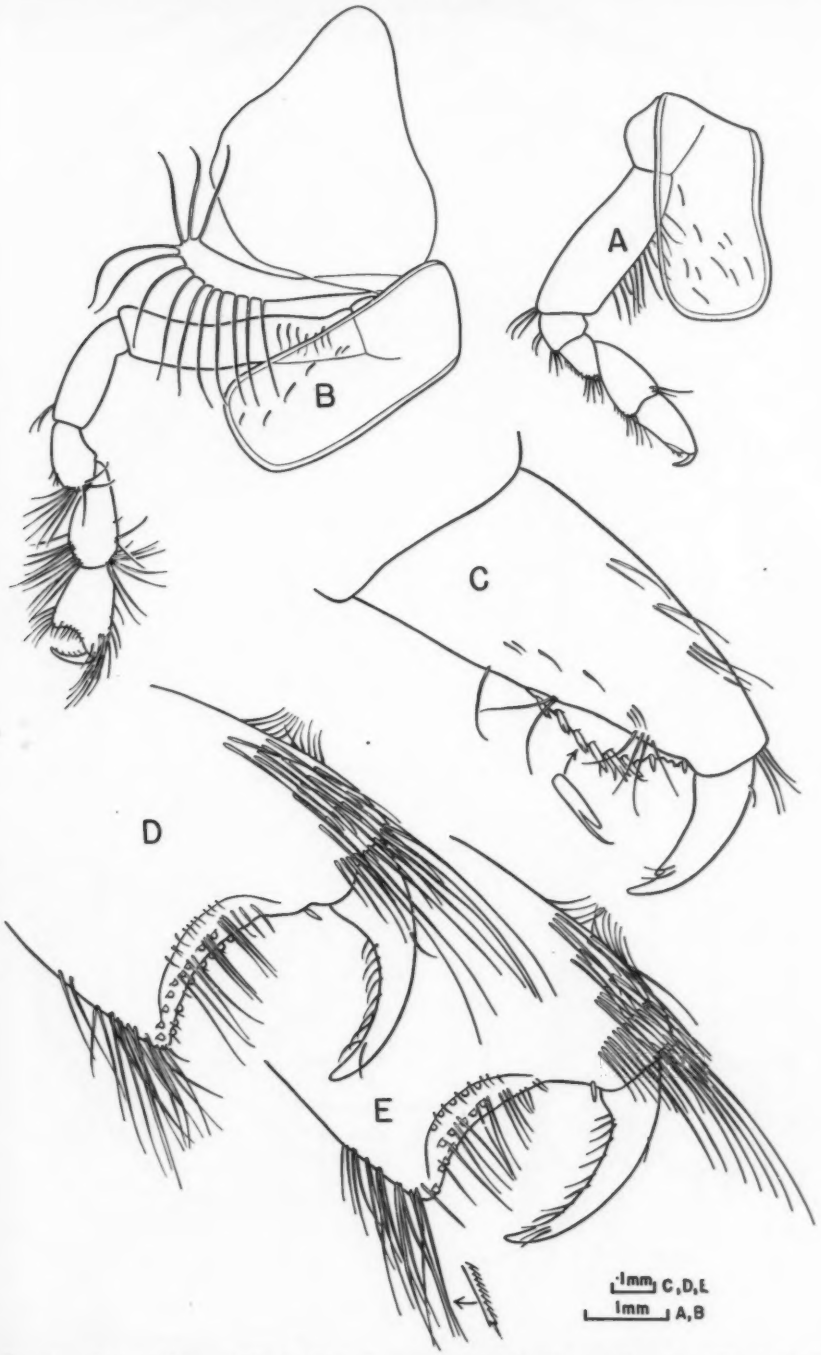

FIG. 44. *Anonyx debruyni* Hoek. A–C, E, mature female, 18 mm, Saguenay Fjord. A, C, peraeopod 1; B, E, peraeopod 2; D, peraeopod 2 of mature male, 20 mm, from Saguenay Fjord.

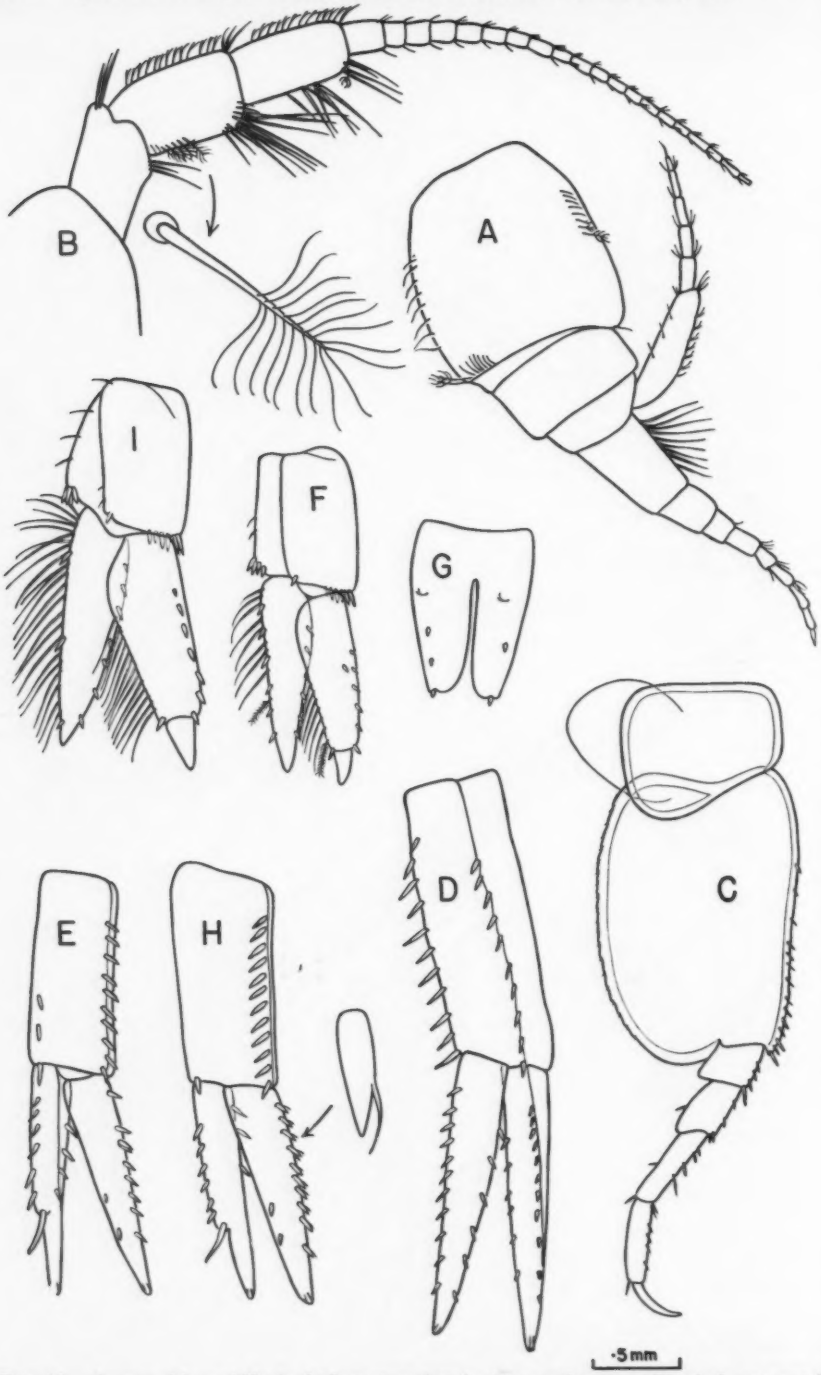

FIG. 45. *Anonyx debruyni* Hoek. A–G, mature female, 18 mm, Saguenay Fjord. A, antenna 1; B, antenna 2; C, peraeopod 7; D, uropod 1; E, uropod 2; F, uropod 3; G, telson; H, I, mature male, 20 mm, Saguenay Fjord; H, uropod 2; I, uropod 3.

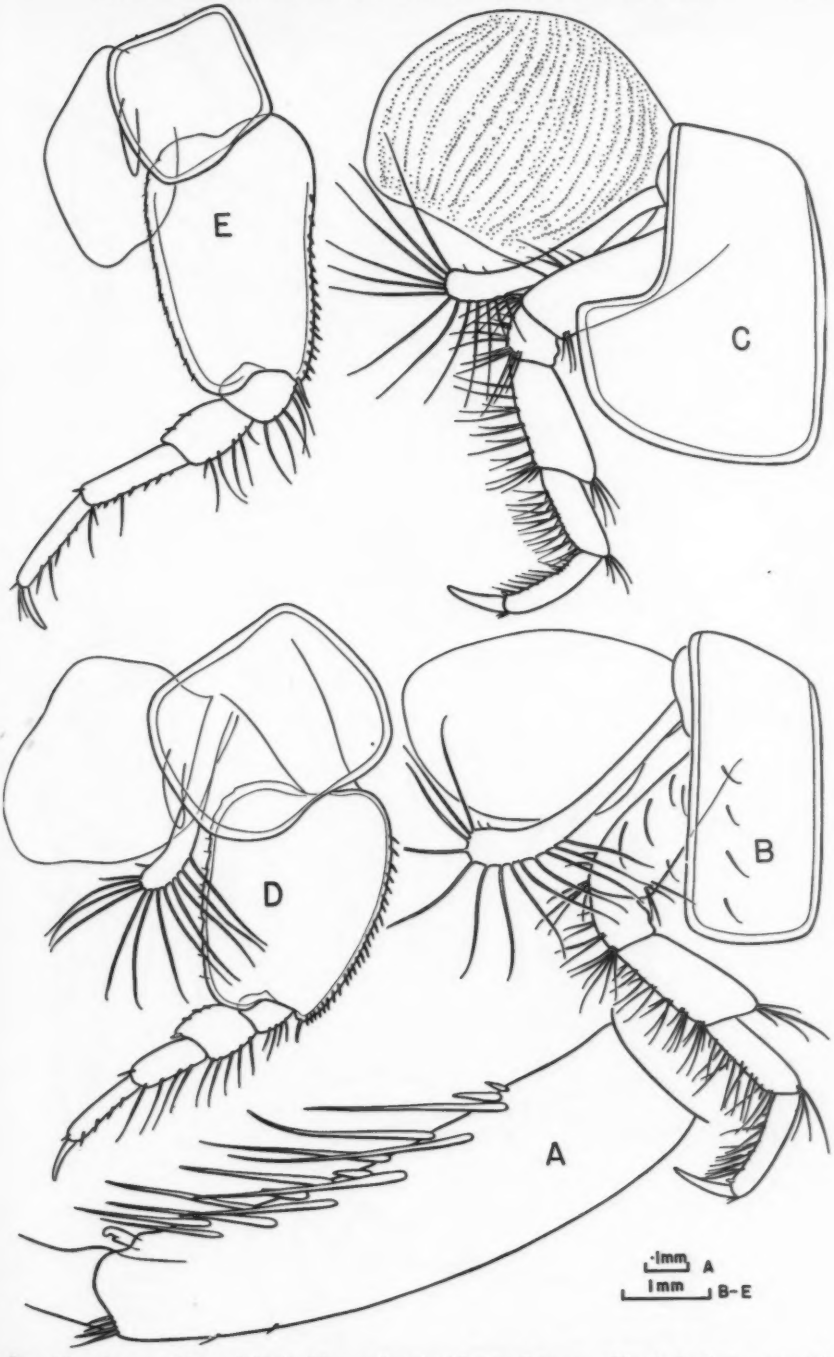

FIG. 46. *Anonyx debruyni* Hoek. Mature female, 18 mm, Saguenay Fjord. A, B, peraeopod 3; C, peraeopod 4; D, peraeopod 5; E, peraeopod 6.

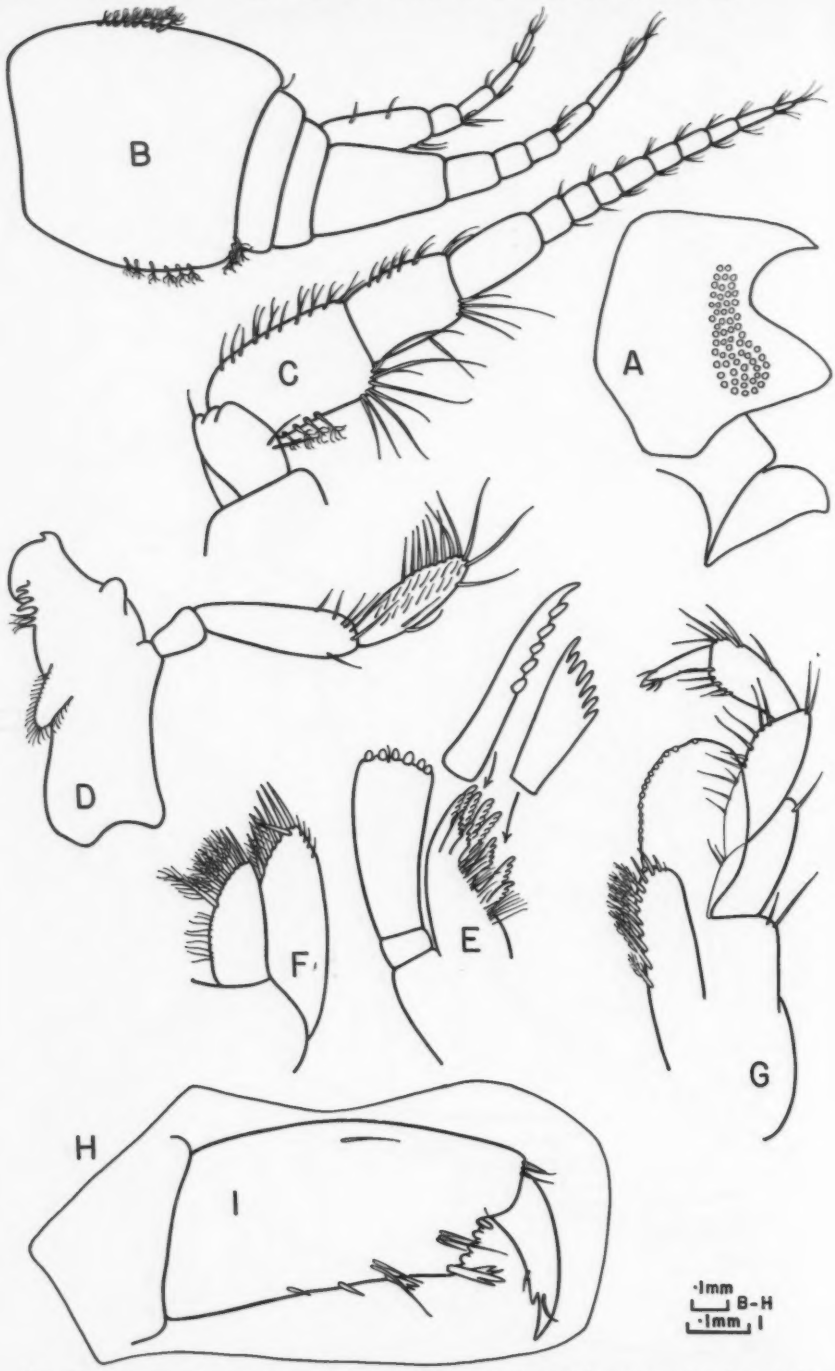

FIG. 47. *Anonyx debruyni* Hoek. Immature, 9 mm, Gulf of Maine. A, head and upper lip; B, antenna 1; C, antenna 2; D, right mandible; E, maxilla 1; F, maxilla 2; G, maxilliped; H, coxal plate 1; I, peraeopod 1.

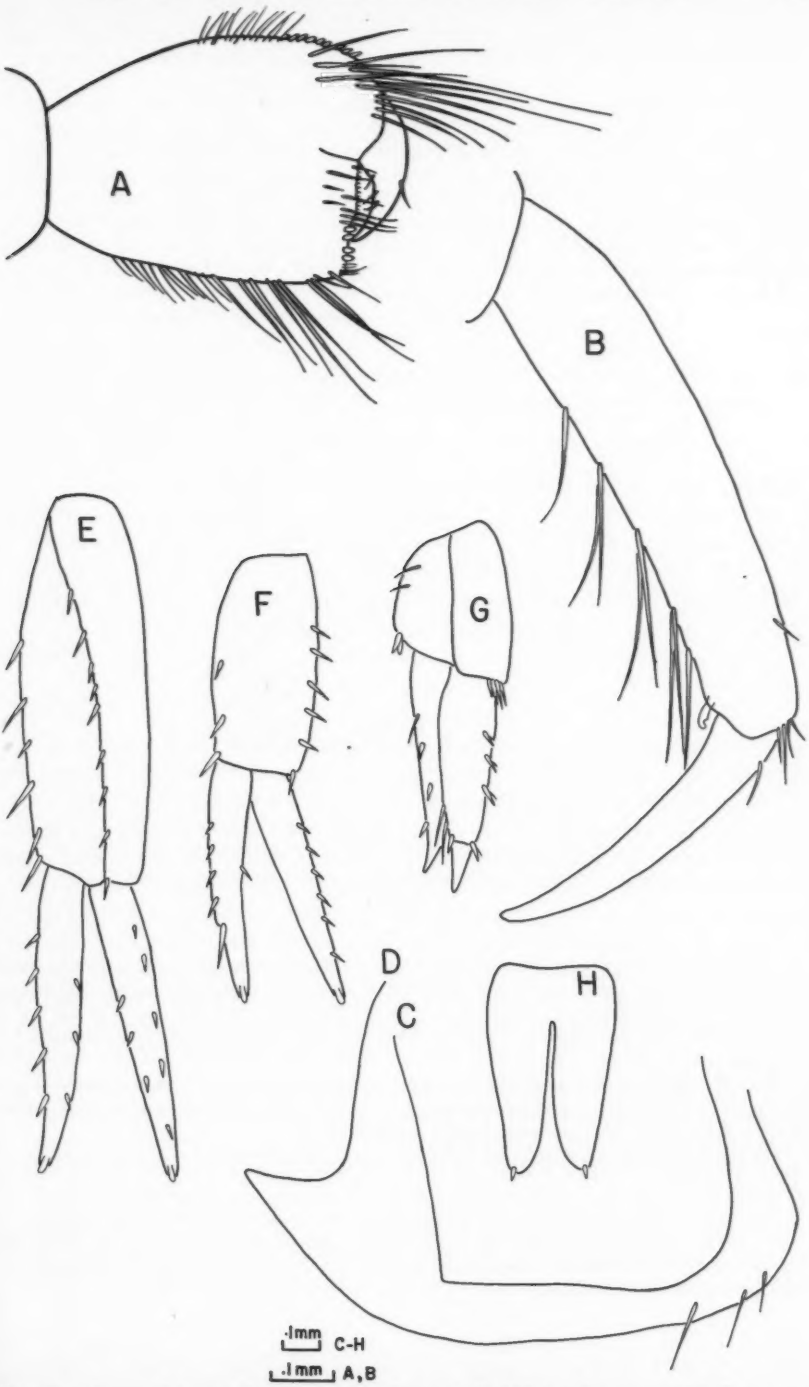

FIG. 48. *Anonyx debruyni* Hoek. Immature, 9 mm, Gulf of Maine. A, peraeopod 2; B, peraeopod 3; C, lateral plate of second metasome segment; D, lateral plate of third metasome segment; E, uropod 1; F, uropod 2; G, uropod 3; H, telson.

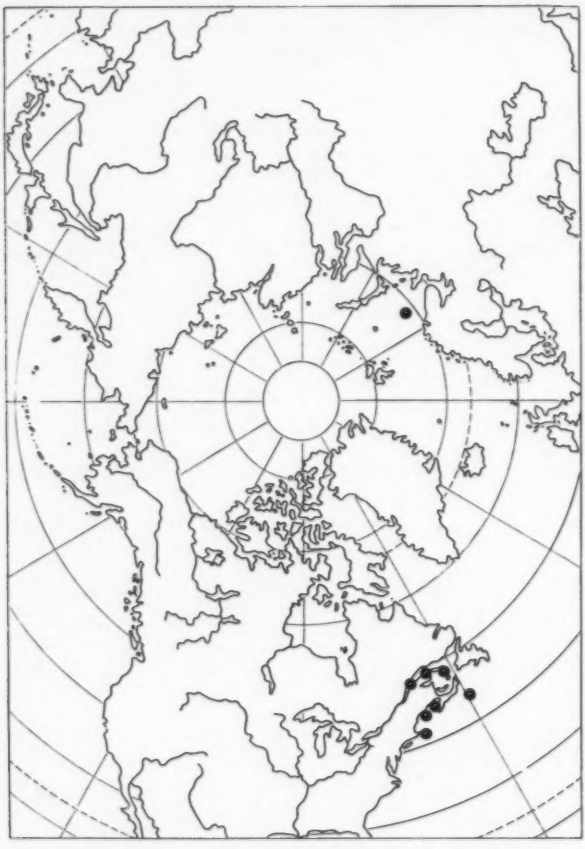

FIG. 49. Distribution of *Anonyx debruyni* Hoek based on examined material.

Uropod 3.—Rami almost equal. Outer ramus broad, tapering from the proximal third, with spines on the inner and outer margins and ventral surface, plumose setae on the inner margin and having a short second segment (one-fifth of the length of the proximal). Inner ramus broad, tapering from the anterior third, with spines on the inner and outer margins and plumose setae on the inner margin.

Telson.—Deeply cleft, bearing a single spine at the apex of each lobe and two small spines and a pair of small setae on the dorsal surface of each lobe. (One specimen has five to six dorsal spines, no dorsal setae and two apical spines on each lobe.)

None of the spines on the uropods and telson are ridged but most have an accessory hair.

MATURE MALE

The mature male is similar to the female except for the antennae which are composed of more and longer segments equipped with calceoli, and uropod 3 which is proportionately larger and more densely setose on the inner margins of the rami. The eye, uropod 2, and peraeopod 2 are the same as those of the female.

YOUNG

The smallest specimens of this species (9 mm) that were examined were readily identified, even though they differed in many respects from the adult.

The interantennal angle of the head is prominent, acutely angled, and has a straight lower edge. The eye is narrow and occupies little of the interantennal lobe. The palp of the first maxilla has only six socketed teeth but also has a seta between the second and the third tooth. The coxal plate of peraeopod 1 is scarcely expanded ventrally; the sixth segment is only slightly narrowed distally; the palm is oblique, relatively broad, and defined by two stout spines with accessory setae; only a few small spines are found on the posterior margin of segment 6; the dactyl, much longer than the palm, bears a prominent tooth and a few setae on its inner margin. The sixth segment of peraeopod 2 is expanded distally but the palm is straight, minutely denticulate, with rounded denticles only towards the posterior corner; the dactyl is of moderate size, with only a few setae on its margin. The other characters are similar to those of the adults.

TYPE-SPECIMEN

Holotype: mature male, 20 mm, Barents Sea (72°32′18″N, 36°39′30″W), July 14, 1879. 128 fath (234 m), second cruise of the *Willem Barents*. Leyden Museum, Leyden, Netherlands.

REMARKS

This species was first described and named *Anonyx debruynii* by Hoek (1882) from a specimen collected in the Barents Sea. Mainly on the basis of the large subchela of peraeopod 2, Sars (1891) placed it in a new genus, *Chironesimus*. With the discovery of a number of Pacific species, many intermediate between typical *Anonyx* and *Chironesimus*, Gurjanova (1962) returned this genus back to *Anonyx*. Hurley (1963) agreed with this decision and so do we.

VARIATION

Gurjanova (1962) has described two subspecies, *debruyni* and *orientalis*, and reported considerable sexual dimorphism in the former. Examination of our specimens has shown that the females resemble those described by Gurjanova, but the males were found to be like the females and quite different from Gurjanova's description. Hoek's type-specimen has been examined and found to be a mature male with elongated antennae equipped with calceoli. As far as could be determined without dissection, this specimen is virtually identical with specimens of this species from the northwestern Atlantic, including those illustrated and described here. It is concluded, therefore, that the males described by Gurjanova possibly represent a distinct species. The presence of sculpturing on the integument, the three keels on the first urosome segment, the rounded second lateral plate of the metasome, the weak constriction of uropod 2, the pleating of the branchial vesicles, and the narrowness of the sixth segment of peraeopod 2, all serve to distinguish her males from the females. However, the structure of peraeopod 2 strongly resembles that of immature specimens and the pleating of the branchial vesicles is also a character which depends upon size. In this connection it should be noted that the description of Sars (1891) was apparently based on small specimens (mature at 14 mm) from the coast of Norway and the differences noted by Stebbing (1894) in the second peraeopods of specimens from the Barents Sea may also

be due to size. In addition, Gurjanova's illustration of a male uropod 2 has many spines and does show a slight constriction and an elongated spine on the inner ramus, characters that were also found in some of the specimens which we have examined.

Gurjanova's (1962) subspecies *A. debruyni orientalis* differs from the typical form in possessing a smaller upper lip, a larger dactyl on peraeopod 2, no constriction on uropod 2, and coarse sculpturing. This is probably a distinct species, although closely resembling *A. debruyni*.

The figures and comments of Stappers (1911) on variations of his small specimens of *Chironesimus debruynii* obviously do not apply to that species, and more probably pertain to *A. compactus* or some species of this complex. His larger specimens apparently belonged to *debruyni*, however.

Distribution

There have been few records of *Anonyx debruyni* in the literature, and those which have been published require confirmation. The material at our disposal did not come from widely distributed localities. The distribution of the species is therefore somewhat uncertain, although it appears that most of the records are from depths of the bathyal zone. In the Gulf of St. Lawrence, for instance, *A. debruyni* is apparently restricted to the third water layer of the Laurentian Channel (and Saguenay Fjord, in ice-cold water, however).

Anonyx compactus Gurjanova, 1962

Synonymy

?Chironesimus debruyni — Stappers, 1911, p. 18 (part), pl. I, fig. 6–8 (not *C. debruynii* Hoek, 1882).

Anonyx compactus Gurjanova, 1962, p. 280, fig. 91A–B.

Anonyx oculatus — Brunel, 1964, p. 3, figure only (not *A. oculatus* Gurjanova, 1962).

Diagnosis of Mature Female

Small, upper lip produced moderately in front of the epistome as an evenly rounded lobe, eye large, anterior lower corner of the first two segments of the flagellum of antenna 1 with a long spine, sixth segment of peraeopod 1 parachelate and dactyl with a long accessory tooth, dactyl and palm of peraeopod 2 fairly long, hind edge of peraeopods 3 and 4 with a row of setae paired with long spines, segment 2 of peraeopod 7 faintly and uniformly serrated on hind edge, as long as rest of limb, inner edge of the outer ramus of the second uropod without spines, inner ramus of uropod 2 completely constricted and bearing a long spine at the level of the constriction, inner edges only of the rami of uropod 3 with setae, posterior projection of the third metasome segment with a straight or strongly concave posterior lower margin, making a distinct, rounded or sometimes sharp angle with the lateral plate.

Description of Mature Female

This is a relatively small species which matures at 12–17 mm. Its integument lacks well-defined sculpturing.

Head.—Relatively small, not much longer than the length of the first segment of the mesosome. Interantennal lobe sharply pointed, forming a right or large acute angle, lower margin straight. Eye large, black or red-brown in colour, broad, expanded ventrally but not occupying all of the interantennal lobe, posterior margin concave and somewhat ill-defined in many individuals.

Antenna 1.—Peduncle long, longer than the head; first segment slightly longer than high, nearly straight in dorsal profile. First segment of the flagellum distinctly conical and elongated, two and a half times as long as its distal diameter, richly supplied with long setae, and armed with a long spine at the inner and lower anterior corner. Second segment of the flagellum armed with a similarly located but shorter spine.

Antenna 2.—Fourth and fifth segments of the peduncle with short setae on their dorsal and long feathery setae on their ventral margin. Flagellum short, with short ventral setae.

Upper lip.—Projecting moderately in front of the epistome as an evenly rounded lobe.

Right mandible.—Three teeth on the cutting edge. Three spine-teeth and seven hairy setules in the spine row. Palp, second segment cylindrical and longer than the third which is densely hairy on the anterior surface.

Left mandible.— Three teeth on the cutting edge.

Maxilla 1.—Outer lobe bearing five small broad spines and six long spines each with two to nine accessory teeth. Palp barely expanded distally, with six small and blunt socketed teeth on tall widely spaced stalks, and an inner unsocketed tooth.

Peraeopod 1.—Coxal plate not expanded anteriorly, but with a concave anterior edge and rounded antero-distal lobe, maximal width almost half as long as the height below the antero-proximal corner. Sixth segment shorter than segment 5, much narrowed distally; palm perpendicular, short and defined by three spines; distal hind edge of the segment with 2–3 similar spines; dactyl much longer than the palm (the appendage is thus parachelate), with a long accessory tooth and a few setae on its inner margin.

Peraeopod 2.—Segment 6 short, slightly more than one half of the length of the fifth, covered distally and ventrally with long pectinate setae with a forked tip; palm perpendicular, long, slightly oblique, bordered with an incomplete series of crowded and acute denticles, defined by an embedded spine more conspicuous than in other species, and not produced under the medium-size dactyl, which has one group of setae on its inner margin.

Peraeopods 3 and 4.—Posterior margin of the sixth segment with a row of setae, each of which is paired with a medial elongate spine; blunt spine at the posterior lower corner of the sixth segment expanded distally and ridged.

Peraeopod 7.—Segment 2, posterior margin with less than 20 low serrations, neither more prominent nor much more crowded in the distal than in the proximal half of the margin; maximal length of the segment about equal to that of the rest of the limb.

Branchial vesicles.—On peraeopods 2–6, transversely pleated on both sides; on peraeopod 7, unpleated; on peraeopods 5 and 6, with an accessory lobe.

Metasome segment 1.—Anterior edge of the lateral plate setose and produced anteriorly at the lower corner.

Metasome segment 2.—Lateral plate setose on the anterior edge, lower posterior corner produced into a relatively small tooth, as compared with that of other species.

Metasome segment 3.—Not carinate dorsally. Lateral plate setose anteriorly and ventrally, posterior projection of moderate size, with a straight or strongly concave posterior margin making a distinct, rounded, or sometimes even sharp angle with the ventral edge of the lateral plate.

Urosome segment 1.—Slightly carinate dorsally and slightly projecting posteriorly.

Uropod 1.—Rami almost equal, with small spines on all margins. Outer edge of the inner ramus with one ridged distal spine and outer margin of the outer ramus with two ridged distal spines.

Uropod 2.—Rami almost equal. Inner ramus completely constricted at about three-fifths of its length, and bearing a long spine at the level of the constriction. This spine is six to seven times the length of the four to six short proximal spines and three-quarters of the distance from its insertion to the end of the ramus. Outer edge of inner ramus with a row of short spines. Outer ramus, outer margin with short spines, of which the distal one is ridged, but without spines on the inner margin.

Uropod 3.—Inner ramus shorter than the outer, tapering from the proximal third, with spines on the margins. Outer ramus also tapering from the proximal third, with a long distal

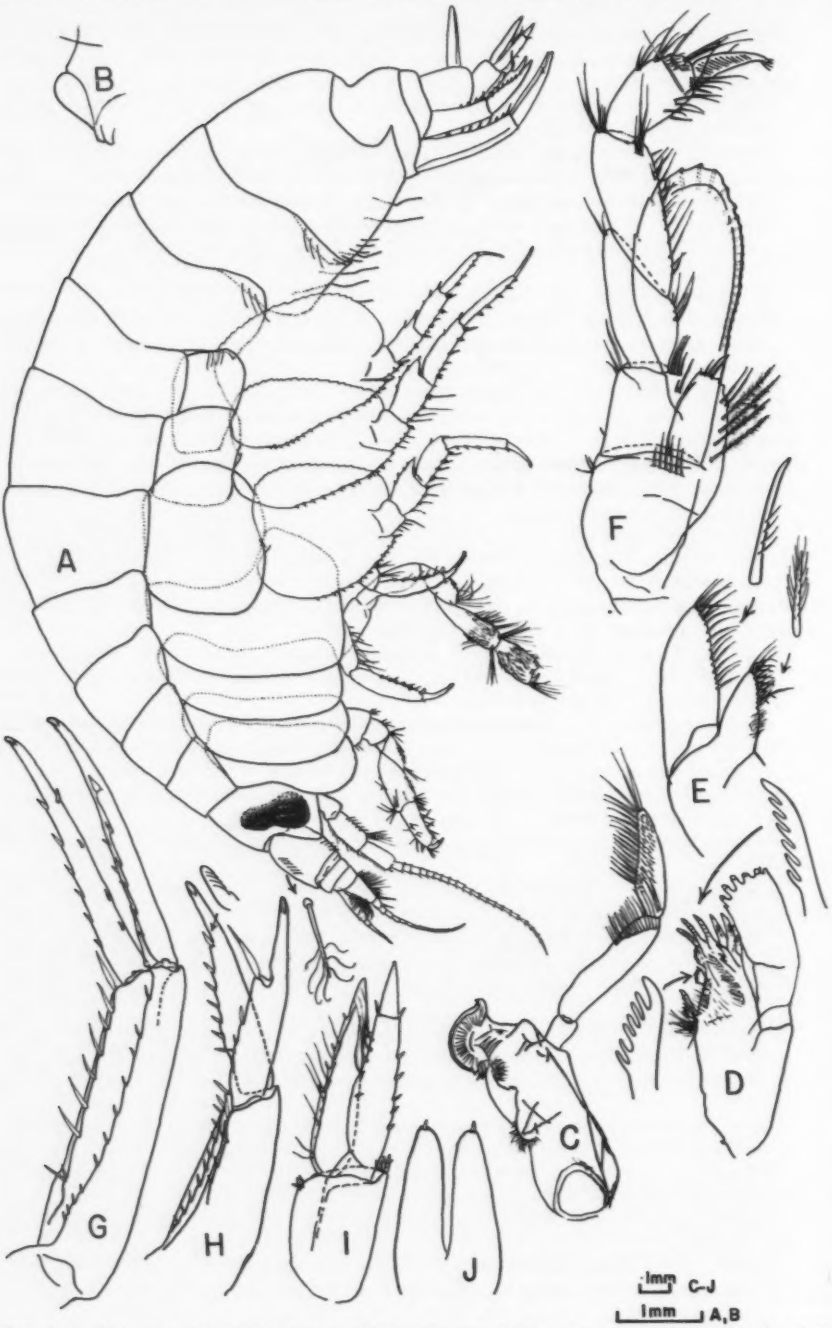

FIG. 50. *Anonyx compactus* Gurjanova. Mature female, 13 mm, Gulf of St. Lawrence. A, whole animal; B, upper lip; C, right mandible; D, maxilla 1; E, maxilla 2; F, maxilliped; G, uropod 1; H, uropod 2; I, uropod 3; J, telson.

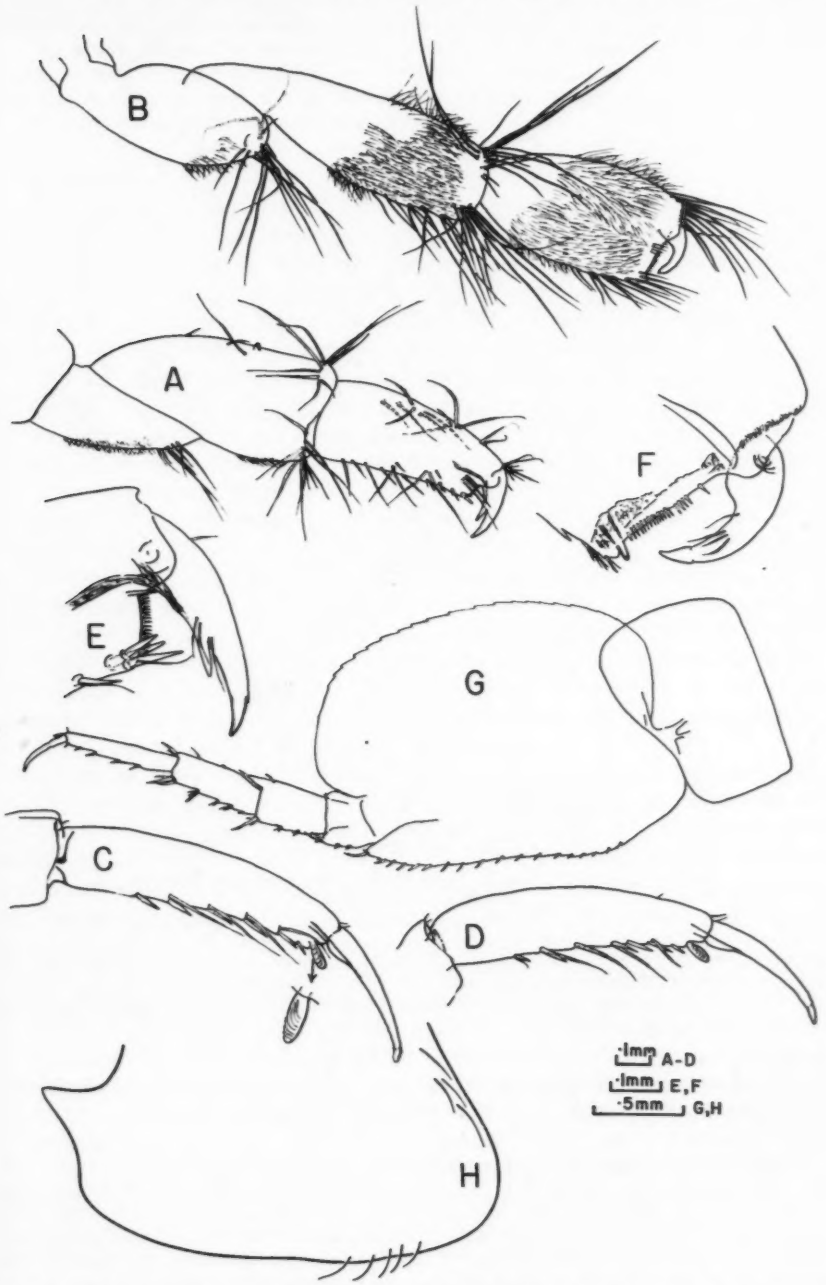

FIG. 51. *Anonyx compactus* Gurjanova. A–G. Mature female, 13 mm, Gulf of St. Lawrence. A, E, peraeopod 1; B, F, peraeopod 2; C, peraepood 3; D, peraeopod 4; G, peraeopod 7; H, lateral plate of second metasome segment of mature male, 17 mm, Fury and Hecla Strait.

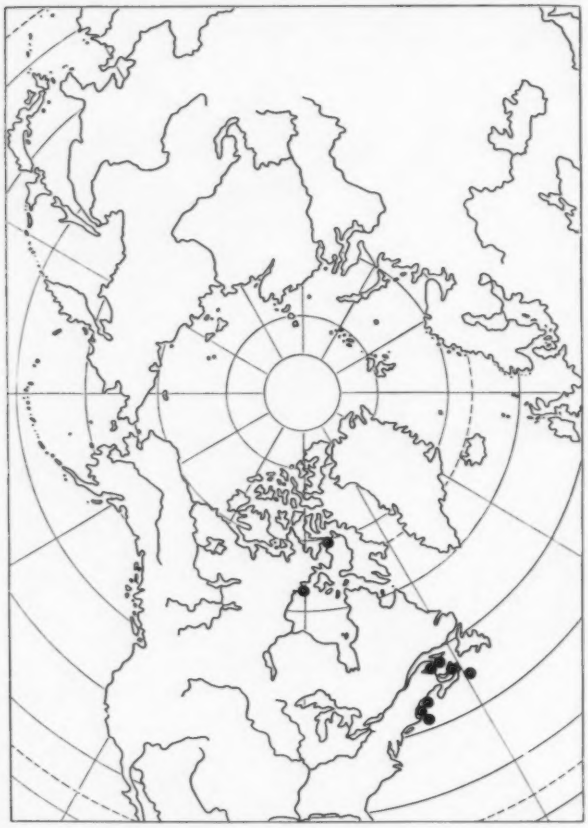

FIG. 52. Distribution of *Anonyx compactus* Gurjanova based on examined material.

segment (one-third to one-quarter of the length of the proximal) and spines on the margins and on the ventral surface. Inner margin of both rami with plumose setae.

Telson.—Deeply cleft, with a single spine and a hair in a notch at the apex of each lobe, but without dorsal spines and setae.

MATURE MALE

The eye is somewhat larger, the antennae have more and longer segments equipped with calceoli and the uropods are better equipped with setae, than in the female.

YOUNG

The smallest specimen of *A. compactus* which we have seen is 3 mm long (Gulf of St. Lawrence, off Cheticamp Is., Sept. 6, 1917). It is too shrunken by alcohol to be drawn profitably, but it was possible to observe the characteristic shape of the third lateral plate of the metasome, already well formed, the equally characteristic distal long spine on the long first flagellum segment of antenna 1, and the long spine and marked constriction of the inner ramus of uropod 2. The second segment of peraeopod 7 is about as long as the distal rest of the limb.

TYPE-SPECIMENS

We have been unable to discover whether type-specimens of *Anonyx compactus* have been designated, or to compare our material with North Pacific specimens identified by the original describer. Several localities in the Okhotsk Sea and elsewhere are given by Gurjanova (1962), so that the type-locality is not known to us either.

VARIATIONS

Our specimens differ as follows from the description and figures of Gurjanova (1962): the upper lip is more produced, there is not any well-developed sculpturing, the first coxal plate is anteriorly concave, the prominent accessory tooth on the dactyl of peraeopod 1 is not divergent, the palm of peraeopod 2 is not convex and the dorsal notch on urosome segment 1 is not so deep. Otherwise there appears to be close agreement.

We are drawing attention below to cases of apparent variations in the diagnostic characters of *A. compactus* which, in our opinion, rather than documenting the variability of the species, point to the existence in the genus *Anonyx* of a complex of species related to *compactus*, several of which have yet to be named and described fully. Since these "variants" occur outside of the geographical area considered in the present work, their further treatment is left for the future.

Anonyx compactus is very closely allied to *A. oculatus* Gurjanova, 1962, and we were at first inclined to identify our specimens with the latter species. However, *A. oculatus* is distinguished by the lack of spines on the hind margin of the sixth segment of peraeopods 3 and 4, the structure of peraeopod 1 (longer palm, parallel sides, and lack of marginal spines on segment 6, and small accessory tooth on the dactyl), the coarser and fewer posterior serrations on segment 2 of peraeopod 7, and the larger eyes.

It seems likely that *A. oculatus* is very close to, if not identical with, the *A. ampulloides* described by Stebbing (1888). This author identified his specimen as *A. ampulloides* Bate, but Bate's type-specimen has proved upon examination to be a young *A. nugax*. The specimen described by Stebbing was searched for in the British Museum but only a vial containing remnants was found. Slide preparations, if such exist, could not be located, so that it is necessary to rely on Stebbing's illustrations and description to establish the identity of his specimen: in our opinion, it belongs to a distinct valid species which, as far as can be determined, is virtually identical with *A. oculatus*. It differs from *oculatus* chiefly in the shape of the third lateral plate of the metasome, in the large number of spines on uropods 1–2 (Gurjanova's specimen was probably immature), in the peculiar shape (possibly crumpled) of the upper lip, and in the presence of spines on the hind edge of the sixth segment of peraeopod 1. (In this Stebbing's species is similar to *A. compactus*.)

Gurjanova (1951) recorded and briefly described specimens which she referred to as *A. ampulloides* Bate, but subsequently (1962) she described them as a new species (*A. derjugini*) and recorded others as belonging to *A. ampulloides* Bate. This last identification was evidently based on Stebbing's (1888) description but her description and illustrations call for two comments:

(*a*) the male (fig. 88A) and the female (fig. 88B) specimens used for the drawings may belong to different species since in comparing the drawings with each other and with the description, differences appear, which would have to be sexual, but of which we have found no examples among the hundreds of specimens of this genus which we have examined from the Atlantic and Arctic regions. For instance, peraeopod 6 (Gurjanova's PpIV) of the female has on segment 2 a postero-distal concavity which is lacking in the male; and uropod 2 is described as having a strongly constricted inner ramus with a long distal spine, which is entirely absent in the illustrated uropod 2 of the male; (*b*) the figure of the female, as far as it goes without referring to that of the male, reveals a species which is close to *A. compactus*, if one may judge by the fairly large eye, the straight interantennal angle of the head, the elongated first flagellar segment of antenna 1, the little-projecting upper lip, the spines on the hind edge of segment 6, and the accessory tooth of the dactyl, of the first peraeopod (Gurjanova's Gp I), and the described (but not illustrated) constricted uropod 2. However, differences with *compactus* appear in the lack of long spines on the first two flagellar segments of antenna 1, expanded first coxal plate, long palm of peraeopod 1, and short segment 2 of peraeopod 7 — shorter than and not as long as the distal rest of the limb — of Gurjanova's species.

One may also refer here to the record by Stappers (1911) of a species close to, if not identical with, *A. compactus*, under the name *Chironesimus debruynii* (Hoek). Stappers, who also had material of the true *debruyni* before him, describes and illustrates for two males three diagnostic features which they share with *A. compactus*, but which may equally apply to *A. oculatus* Gurjanova. These specimens came from the Murman Sea.

Finally, one of us (P.B.) has seen a specimen from Alaska, in the U.S. National Museum material, which is remarkably close to *A. compactus*, except that the second peraeopod has a chela as small as that of *A. lilljeborgi*, and that the third metasome lateral plate is scarcely angular at the junction with its posterior projection.

Distribution

Gurjanova (1962) mentions several localities from the Sea of Japan to Kamchatka, in the Okhotsk Sea, where *A. compactus* was taken; although the available records of this species from the North Atlantic Ocean and arctic regions are still sparse, the evidence up to date indicates that it may be another species of Pacific origin which has spread into the western Atlantic, but has not yet reached the eastern Atlantic (see however the possible record of Stappers, 1911, discussed above). On the other hand, like other species of this biogeographic category, it seems to prefer very cold water such as that of the intermediate cold layer in the Gulf of St. Lawrence, and this may also explain its absence from the eastern Atlantic.

LIST OF SPECIES EXCLUDED FROM THE GENUS *ANONYX*

We exclude the following species from the genus *Anonyx*, as defined above with old and new probable generic characters, our evidence being indicated as from the original description (D) and figure (F), a subsequent description (D2) and figure (F2), and our examination of type-specimens (T). Species are not listed on which we have no new evidence, and whose status has previously been discussed and generally accepted in the literature. More details on our evidence can be found in the following annotated bibliography.

Name	Evidence	Present status
Anonyx nobilis Stimpson, 1853 (transferred to *Chironesimus* by Barnard, 1962) (see Bate, 1862)	D,D2,F2	? (*"Tmetonyx"*) (Shoemaker, 1930a)
Anonyx politus Stimpson, 1853	D,F2	*?Tmetonyx cicada* (Bate, 1862; Stebbing, 1906)
Anonyx Fuegiensis Dana, 1853 (see Bate ,1862)	F2	?
Anonyx punctatus Bate, 1862	D	?
Anonyx annulatus Bate, 1862	D,F	?
Lysianassa martensi Goës, 1866 (transferred to *Anonyx* by Boeck, 1870)	T	?
Anonyx wolfendeni Tattersall, 1909	D,F	?
Lakota adversicola K. H. Barnard, 1925 (transferred to *Chironesimus* by Schellenberg, 1926, and Barnard, 1940)	D,F2,T	?
Lakota rotundatus K. H. Barnard, 1925 (transferred to *Chironesimus* by Barnard, 1940)	D,F2,T	?
Anonyx dorotheae Hurley, 1963	D,F	*Schisturella*

CHRONOLOGICAL ANNOTATED BIBLIOGRAPHY

Since the species *A. nugax* and the genus *Anonyx* are among the very oldest of their category in the Amphipoda, the published record is very extensive and the nomenclatural as well as the taxonomic problems are many. In order to deal adequately with the species found in the northwestern Atlantic, it has been necessary to consult all of this vast literature. The results of this review of the important references to this genus are summarized here. Further details may be found by referring to Stebbing (1888, 1906) and Barnard (1958).

PHIPPS, C. J., 1774

Phipps briefly describes and illustrates under the Insecta two species of Amphipoda which he names *Cancer nugax* and *Cancer ampulla*. The type-specimen of *Cancer nugax*, which was trawled near Moffen Island, off the north coast of Spitzbergen, has never been reported since and must be presumed to be lost. Phipps' description is too brief and his illustration too generalized for this specimen to be identified with certainty in spite of the assertions of later authors. Nevertheless, it was probably identical with the form to which, with the majority of authors since Miers (1877a), we refer in the present work as *Anonyx nugax* (Phipps), which is the common large species of this genus at Spitzbergen.

FABRICIUS, J. C., 1781

Cancer nugax Phipps is transferred to the new genus *Gammarus*.

SABINE, E., 1824

Sabine notes that the specimens of *Cancer nugax* which were collected should be referred to as *Gammarus nugax*. These were subsequently incorrectly referred to *Lysianassa vahlii* by Goës (1866) because Bate (1862) considered them to be identical with his *Lysianassa nugax*, which he had originally described as *Lysianassa bidenticulata* (Bate, 1858).

PARRY, W. E., 1824

No collections are listed for this expedition but Parry does note in the text the abundant occurrence of small shrimp, presumably *A. nugax* (Phipps), and their voracity as follows: "I have before mentioned the myriads of small shrimps (*Cancer nugax*), which for some weeks past had been observed near the surface of the sea. These insects were found to be still as numerous as ever in any hole we made in the ice; and such was the extreme avidity with which they immediately seized upon any meat put overboard to thaw or soak for the sake of freshness, that Captain Lyon today sent me a goose to look at, belonging to the officers of the Hecla, that had been thus deposited within their reach only eight and forty hours, and from which they had eaten every ounce of meat, leaving only a skeleton delicately cleaned. Our men had before remarked that their meat suffered unusual loss of substance by soaking, but did not know to what cause to attribute the deficiency."

ROSS, J. C., 1826 AND 1828

In these publications the specimens collected are listed as *Talitrus nugax*. They were also mistakenly referred to *Lysianassa vahlii* by Goës (1866).

LATREILLE, P. A., 1829

Latreille suggests that *Gammarus nugax* (Phipps) possibly should be placed in the genus *Atylus*.

ROSS, J. C., 1835

The specimens collected on this expedition are listed as *Gammarus nugax* by Ross. However, Bate (1858) later used one which he thought was collected on this expedition to describe *Lysianassa bidenticulata*. He subsequently (1862) referred this specimen to *L. nugax* on the mistaken assumption that it was identical with Sabine's specimens. Bate's species was considered a synonym of *vahlii* by Goës (1865) and Boeck (1870). It was recognized as a valid species by Miers (1877a) and placed in the genus *Socarnes* by Sars (1885).

A numbers of Ross' collections are preserved in the British Museum (Natural History). These were examined and found to consist mainly of *A. nugax* (Phipps), although *A. lilljeborgi* is also present. Unfortunately, the exact source of these collections is unknown.

KRØYER, H. N., 1838a

In this paper Krøyer describes in considerable detail and illustrates three new species, *Vahlii* Reinhardt, *Lagena* Reinhardt, and *appendiculosa* n.sp. which he at first places in Milne-Edwards' genus *Lysianassa*. However, he subsequently remarks that they can be placed in this genus only with difficulty and therefore proposes a new genus, *Anonyx*, so named because of a supposed lack of dactyl on peraeopod 2, for their reception. Our examination of the latter two specimens has shown them to be typical *Anonyx nugax* (Phipps) as described and illustrated here. However, other specimens from northern Norway that were identified by Krøyer were found to be *A. lilljeborgi*. *Lysianassa vahlii* is a distinct species now known as *Socarnes vahli* (Krøyer).

KRØYER, H. N., 1838b.

His two new species are listed here as *Anonyx lagena* and *Anonyx appendiculosus*.

MILNE-EDWARDS, H., 1840

Milne-Edwards places Krøyer's species in his genus *Lysianassa* as *L. lagena* and *L. appendiculata* respectively. *Cancer nugax* Phipps, he notes, may also belong to *Lysianassa* but he considers it too poorly known to be assigned exactly.

KRØYER, H. N., 1842

Krøyer notes that he has discovered that male amphipods are often distinguished from the females in having calceoli on their antennae and much longer second antennae. He concludes,

therefore, that *A. appendiculosus* is only the male of *A. lagena*, although the type-specimen of *A. lagena* has also proved to be a male, badly broken and eviscerated as if by digestion and having lost all antennal flagella. Since Krøyer's (1838a) fig. 1 of *Lysianassa lagena* shows entire antennae, the Umanak types must have been damaged subsequently, or Krøyer confused immature males with females. These sexual differences have been confirmed here in all of the species of the genus *Anonyx* that we have studied and appear to be common in other genera of the family Lysianassidae. Unfortunately this has not always been properly appreciated even in recent publications.

Krøyer also notes that species of *Anonyx* do have a dactyl on their second peraeopods but rejects the fusion of *Anonyx* with *Lysianassa* because of other differences in the structure of this peraeopod.

KRØYER, H. N., 1845

Having apparently become aware of Phipps' publication, Krøyer fuses his *Anonyx lagena* with *Cancer ampulla* Phipps under the name *Anonyx ampulla*. Differences in their morphology he ascribes to the fact that Phipps' specimen came from a seal stomach and that the description and figures of *Cancer ampulla* were imprecise. *Cancer nugax* he considers also to be an *Anonyx* but believes it to be a doubtful synonym of *ampulla*. Consequently, he now refers to his specimens as *Anonyx ampulla* Phipps, and describes them in great detail.

KRØYER, H. N., 1846

In this paper Krøyer presents a Latin diagnosis of *Anonyx ampulla* Phipps.

KRØYER, H. N?, 1846?

The figures of the amphipods in this atlas have been generally ascribed to Krøyer even though their true authorship is uncertain (Stebbing, 1888). Figure 2 of plate 13 illustrates *Anonyx ampulla* Phipps in considerable detail, even to including the long spine of the inner ramus of uropod 2. There is now little doubt that the figures represent *A. nugax* (Phipps): the two Copenhagen Museum specimens from Spitzbergen (labelled "TYPER, Krs' Originalex"), which presumably served as models (at least for the external appearance since they are not dissected) actually proved upon our examination to belong respectively to *A. nugax* and *A. laticoxae*, the latter species not having any constriction and long spine to uropod 2.

STIMPSON, W., 1853

Four new species of Amphipoda are described as belonging to the genus *Anonyx*: *nobilis*, *politus*, *pallidus*, and *exiguus*. No illustrations are given, and the descriptions are rudimentary. The first species is now known as *Tmetonyx nobilis*, recognized by Shoemaker (1930a). *Anonyx politus* is considered as identical to *Tmetonyx cicada* by Bate (1862) on the basis of the description only, but is retained as a doubtful species of Lysianassidae by Stebbing (1906). The "bright red colour" of its eyes would exclude it from *Anonyx*, in our opinion. Of the other two species, Bate (1862) endorses both but has seen and illustrates only the last, whereas Stebbing (1906) leaves both in doubt, where they have remained ever since. *Anonyx exiguus* remains doubtful; in our opinion, *A. pallidus* is possibly the species which we describe here as *A. sarsi*, although our uncertainty justifies this new name, as discussed above.

BELL, T., 1855

The specimens collected are listed as *Lycianassa lagena* Krøyer.

BRUZELIUS, R. M., 1859

The genus *Anonyx* is described in detail and *Anonyx ampulla* (Phipps) is listed together with a detailed account of its synonymy.

BATE, C. S., AND J. O. WESTWOOD, 1861

The species described and figured as "*Anonyx ampulla* Krøyer" is now known as *Tryphosites longipes* (Bate & Westwood), following Boeck (1870) and Sars (1891).

BATE, C. S., 1862

In the genus *Anonyx*, Bate lists and describes briefly 21 species, of which 7 have not been satisfactorily dealt with subsequently, by removal to other newly created or better defined genera.

All but one (*ampulloides*) of these species are listed as doubtful by Stebbing (1906), and may be commented upon briefly as follows: (1) *A. exiguus*, *politus*, and *pallidus*, described by Stimpson, 1853, and apparently endorsed by Bate, are discussed above (cf. Stimpson); (2) *A. ampulloides* n.sp. from the Sea of Japan, upon our examination of the type-specimen in the British Museum, has proved to be a young *A. nugax*; (3) *A. punctatus* n.sp. from Bering Strait, described as having the "eyes small, round, red," is evidently not an *Anonyx*, but still cannot be identified; (4) *A. annulatus* n.sp. from Japan, is considered as possibly a *Tryphosa* by Stebbing (1906). From its rounded third metasome lateral plate we would exclude it from *Anonyx* but cannot be more accurate as to its identity; (5) *A. Fuegiensis* Dana from Tierra del Fuego, certainly not an *Anonyx* from its distribution and lack of projection on the third lateral plate of the metasome, is left in doubt by Stebbing (1906). We cannot do better.

On the other hand, Bate's *A. ampulla* Krøyer is evidently *Tryphosites longipes* and his *Lysianassa nugax* (Phipps), which is the name he applies here to his *Lysianassa bidenticulata* Bate, 1858, and which he equates incorrectly with Phipps' species, is *Socarnes bidenticulatus*. His *A. lagena* Krøyer and *Lysianassa appendiculata* are probably *A. nugax* (Phipps), although one Bering Strait specimen with the former label collected by Stimpson proved to be *A. laticoxae*.

LILLJEBORG, W., 1865

Anonyx ampulla (Phipps) is listed and the right mandible is illustrated in detail. Lilljeborg also notes that *Anonyx ampulla*, i.e. *Anonyx nugax* (Phipps), is misidentified by Bate and Westwood, and does not appear in their monograph of 1861.

GOËS, A. T., 1866

Goës lists *Lysianassa lagena* Krøyer and describes a new species, *Lysianassa martensi*. Since the latter species was later placed by Boeck (1870) in the genus *Anonyx* where it has remained since, the type specimen has been examined. Although this has revealed that it is not an *Anonyx*, it has not been possible yet to refer it to any genus.

BOECK, A., 1870

The genus *Anonyx* is described in great detail and its characterization made more precise, with the result that many of its species are removed to other genera. Under *Anonyx*, Boeck lists *A. lagena* Krøyer, *A. martensi* Goës, and *A. lilljeborgi*, a new species which he describes briefly. A paratype of the latter species has been examined and found to be similar to specimens from the northwestern Atlantic which are illustrated and described here under Boeck's name, which is thus valid.

BOECK, A., 1872, 1876

This posthumous work contains a more detailed treatment, with illustrations, of the account of this genus which appeared in 1870.

BUCHHOLZ, R., 1874

Buchholz lists his specimens as *A. lagena* Krøyer and notes that free-living young, 3.2 mm long, which he considers to be the newly hatched young of this species, are generally similar to the adults but have very short antennae, linear red eyes, and right-angled corners on the third lateral plates of the metasome. The last character is, however, not found in young *Anonyx*, which suggests that he may have based his observations on the young of some other species.

HELLER, C., 1875

Heller describes and illustrates large (40–50 mm) specimens, most probably *A. nugax* from their size, which he calls *A. lagena* Krøyer. The mandible is described in detail and he notes that the left has two teeth and the right only one tooth on the cutting edge.

STEBBING, T. R. R., 1876

Stebbing here expresses dissatisfaction with the unreliability of Boeck's characters to distinguish the genus *Orchomene* (then including *Orchomenella*) from the genus *Anonyx*. This situation was later improved by Sars (1891), and accepted by Stebbing (1906) himself. Stebbing

also insists on the unreliability of characters linked to sex (length of antennae, setose third uropods) and size (proportion of limb segments, and possibly eye colour) for separating species.

MIERS, E. J., 1877a

In this paper Miers has this single comment: "Phipps' figure of this common Arctic species is quite recognizable and his name must therefore be adopted for it." He accordingly lists as *A. nugax* (Phipps) his specimens, which we have examined: we are in agreement with his designation. However, as pointed out previously, with the subsequent description of many new species, Phipps' illustration is no longer recognizable as this species. It is the distribution of the various species which makes it likely that it represents the animal here identified as *A. nugax* (Phipps).

Miers also notes that *Lysianassa bidenticulata* (Bate, 1858), which was subsequently referred to Phipps' species by Bate (1862), is a valid species distinct from *Socarnes vahli* (Krøyer).

MIERS, E. J., 1877b

In reporting upon the collections of *A. nugax*, Miers notes: "my observations scarcely agree with those of Hr. Buchholz and other authors as regards the rare occurrence of the males of this very common and well-known Amphipod." He also observes that they are distinguished from the females by the longer flagella of the inferior antennae which, when drawn back, reach to the posterior margin of the seventh segment of the body.

LOCKINGTON, W. N., 1877

Lockington describes very briefly a dried specimen from western Alaska, which he names *Lysianassa Fisheri*, and which Holmes (1904) later examined and assigned to the species *Anonyx nugax*. This cannot be confirmed since the type was lost in the San Francisco fire of 1906 (Allyn G. Smith, personal communication).

HOEK, P. P. C., 1882

In this paper Hoek lists collections of *Anonyx lagena* Krøyer and then describes as new *Anonyx debruynii* on the basis of a single specimen. This type-specimen has been examined and found to be a mature male, similar, as far as can be determined, to the specimens from the northwestern Atlantic that are described here under the same name.

SCHNEIDER, J. S., 1884

Schneider gives a few pieces of information (size, shallow habitat) on "*Anonyx lagena* Krøyer" from the Tromsø area in northern Norway, indicating that he was most probably dealing with *A. sarsi*. After noting that his material agrees in general with the information given by Heller (1875), he describes characters not noted previously, especially the proximal hair tuft of the outer lobe of maxilla 1 (although he saw only 9 toothed spines on the lobe), the distal spine on segment 6 (which he counts as fifth) of peraeopods 3–4, and the constriction and spine of the inner ramus of uropod 2.

HANSEN, H. J., 1887

Hansen gives many localities for *Anonyx lagena* in West Greenland. He notes that Krøyer's (1838a) type specimens from Umanak are not in the Copenhagen Museum, but that other specimens of Krøyer from Norway and Spitzbergen are available. Dr Torben Wolff has recently discovered the Umanak types in the Copenhagen collections and kindly let us examine them, in addition to those of Spitzbergen (also labelled "Types"). The former two specimens proved to belong to the same species, here called *A. nugax*, whereas the two Spitzbergen ones are *nugax* and *laticoxae* Gurjanova, 1962.

STEBBING, T. R. R., 1888

In his bibliography Stebbing discusses the systematics of the genus *Anonyx* and its known species and in the text describes and illustrates in detail a species collected in the Sea of Japan which he identifies as *Anonyx ampulloides* Bate, 1862. As pointed out above, only remnants of his specimen were found. His description and figures show that his species is not *A. ampulloides* Bate but has probably been redescribed by Gurjanova (1962) under the name of *A. oculatus*. This latter name may therefore stand for this species, pending further information on the differences still observed (see above) between the two descriptions and figures.

VOSSELER, J., 1889

Vosseler here describes a new species which he names *A. kukenthali*. The description and illustrations, brief as they are, offer no reason for not accepting them as *A. nugax* (Phipps). Vosseler's specimens, the largest of which was 22 mm, were probably re-identified later as *A. nugax*: material from the expedition which is labelled as such is kept at the Hamburg Zoological Museum, despite the fact that *A. nugax* is not listed by Vosseler although, as pointed out earlier, it appears to be the common species at Spitzbergen and would in all probability have been collected.

SARS, G. O., 1891, 1895

The genus *Anonyx* is defined in the manner of Boeck (1870) but with considerably more precision and detail, so as to exclude better than previously a group of species in the genera *Orchomene*, *Orchomenella*, and *Orchomenopsis*. On the basis of simple gills, of the large, produced upper lip, and of the powerful peraeopod 2, Sars separates from *Anonyx* a new genus *Chironesimus* to receive Hock's species *debruynii*. Probably because of the small size of the specimens which he examined, the hand and the dactyl of peraeopod 2 are described as being coarsely denticulate. In large specimens, only setae and nodular spines are found (see also Stebbing, 1894).

In the genus *Anonyx*, Sars (1891) lists *A. nugax* (Phipps), as the senior synonym of Krøyer's *Anonyx lagena*, and *A. lilljeborgi* Boeck. Later (1895), however, he notes that arctic specimens of the former differ from those of the Norwegian coast in size and in the relative lengths of the fifth and sixth segments of peraeopod 1. He suggests that the latter specimens may prove to be specifically distinct and should be called *A. lagena*. However, examination of Krøyer's types showed them to be typical *A. nugax* (Phipps) and his Norwegian specimens to be *A. lilljeborgi*, so that there is no reason to suggest that Krøyer's *lagena* is identical with Sars' Norwegian specimens. Nevertheless, there is reason to believe that Sars was right in believing his specimens to constitute a distinct species. This has been described here as *A. sarsi* to honor his recognition of this form and his tremendous contributions to the study of amphipods. It should be emphasized, however, that the relative lengths of the segments in peraeopod 1 vary with the size of the individual and are of little value in distinguishing this species.

STEBBING, T. R. R., 1894

Stebbing records specimens of *A. nugax* (Phipps), *A. lilljeborgi* (Boeck), and *Chironesimus debruynii* (Hoek). However, in the discussion of *A. lilljeborgi* he points out that the distinctions described by Boeck (1870) and Sars (1891) are minor and may be due to the small size of this species. Only the greater projection of the hand of peraeopod 2 and the relatively larger size of the blunt spine at the base of the dactyl on peraeopods 3 and 4 are, in his opinion, of specific importance. Even these vary with size, as is shown in the present paper. Nevertheless he writes: "I retain Boeck's species for the moment as the most convenient way of calling attention to the subject, but my own conviction is that *Anonyx lilljeborgi* is only a small form of *Anonyx nugax*." Stebbing is apparently responsible, therefore, for the idea that *A. lilljeborgi* is only a young *A. nugax*, a view that persisted for a number of years. In this paper he calls attention to the constriction and long spine on the inner ramus of uropod 2 in both *A. nugax* and *A. lilljeborgi*, characters that were omitted by Sars (1891) in his description and figures, but had been independently observed by Schneider (1884).

Discussing *C. debruynii*, he notes that the palm of peraeopod 2 is covered with setules and blunt spines, presumably like those found in the specimens illustrated here.

OHLIN, A., 1895a

After listing a number of collections of *Anonyx nugax* (Phipps), Ohlin describes a new species, *Anonyx affinis*, from four small specimens collected off Cape Dudley Digges, West Greenland. Unfortunately the type-specimens could not be located and the descriptions and figures are not precise enough to allow these specimens to be identified with certainty. According to Ohlin, *A. affinis* is distinguished by large, black, kidney-shaped eyes, a keeled first urosome segment, and an inner ramus of uropod 3 which is shorter than the outer by one third. However, these characters are found in other *Anonyx* species (although the urosome keel, to attract Ohlin's

attention, may be supposed to have been larger than in other species, as it is in *A. ochoticus*), and a relatively short inner ramus of uropod 3 is a common feature of young specimens of *Anonyx*. Therefore, unless the type-specimens of *A. affinis* can be found and re-evaluated, this species must retain a doubtful status as a possible synonym of *A. ochoticus*.

Gurjanova (1951, 1962) has referred North Pacific specimens to *A. affinis* apparently on the basis of the urosome keel and structure of the third uropods, but there appears to be little justification for this identification.

OHLIN, A., 1895b

In this paper Ohlin notes that *A. affinis* may possibly be a synonym of *A. kukenthali*, but this is improbable because of the size difference between the two species (13 vs. 22 mm). He adds nothing that would improve his earlier description.

NORMAN, A. M., 1900

Norman follows Stebbing (1894) and considers *A. lilljeborgi* to be the young of *A. nugax* (Phipps), although he does not list the former in his synonymy. He points out correctly that the relative size of the blunt spine on the sixth segment of the third and fourth peraeopods varies with size and that its presence is not a valid character of *A. lilljeborgi*. His collections in the British Museum have been re-examined. His small specimens from Norway include both *A. lilljeborgi* and *A. sarsi* but his large arctic specimens are mostly *A. nugax* (Phipps). In addition, the specimen (20 mm) from the Firth of Forth is also *A. sarsi*. Therefore *A. nugax* has still not been found south of the Wyville Thompson Ridge.

HOLMES, S. J., 1904

Holmes notes that he has re-examined Lockington's (1877) type of *Lysianassa Fisheri* which was collected on the western coast of Alaska. He reassigns it to *Anonyx nugax* (Phipps). This may be correct but in view of the loss of the holotype, the available information and figures are not extensive enough for a positive identification.

HOLMES, S. J., 1905

Anonyx sarsi is briefly described and illustrated under the name of *A. nugax*, but can be identified only by the photograph (plate III), size, and distribution.

STEBBING, T. R. R., 1906

The genera *Anonyx* and *Chironesimus* are described concisely after Sars (1891). Stebbing recognizes five valid species in the genus *Anonyx*: *nugax* (Phipps), *lagena* Krøyer, *affinis* Ohlin, *lilljeborgi* Boeck, and *ampulloides* Bate. *Anonyx lagena* is recognized as a valid species apparently on the basis of the suggestion of Sars (1891, 1895) and distinguished by the relative length of segments 5 and 6 in the first peraeopods. *Anonyx kukenthali* Vosseler is listed as a synonym of *A. lagena*. Stebbing lists as doubtful 18 names previously referred to *Anonyx*, plus *Lysianassa Fisheri* Lockington and *L. martensi* Goës. We have comments on only 7 of these names.

BRÜGGEN, E. VON DER, 1907

Brüggen shows that the length of the fifth segment of peraeopod 1 is less than that of the sixth segment in small specimens (7 mm) but increases with size so that it is greater in large specimens (35 mm). He concludes, therefore, that *A. lagena* Krøyer as distinguished by Sars (1891, 1895) and Stebbing (1906) is a synonym of *A. nugax* (Phipps).

HOLMES, S. J., 1908

Included is a new genus and species, *Lakota carinata*, collected off the coast of California. This genus has been submerged into *Anonyx* by Hurley (1963) and our examination of the type-specimen has shown that it is merely a specimen of *A. lilljeborgi* Boeck. A re-description and new illustrations will be published elsewhere by one of us (P.B.).

TATTERSALL, W. M., 1909

Tattersall describes *Anonyx wolfendeni* from a single specimen collected in the North Atlantic in 600–700 fath. It differs in so many characters — including lack of eyes, lateral head

lobes, posterior projection of the third lateral plate of the metasome, produced epistome, and half-cleft telson — that it obviously cannot be referred to *Anonyx* as defined here. Tattersall was uncertain of its generic position in this original description. It is still difficult to know where it should be placed even now without examination of the specimen.

STAPPERS, L., 1911

Stappers gives added support to Brüggen's conclusion (1907) that *A. lagena* Krøyer is a synonym of *A. nugax* (Phipps) and also agrees with Stebbing's idea that *A. lilljeborgi* is the young of *A. nugax*. He also mentions six specimens of *Chironesimus debruynii* (Hoek), but his figures and comments make it clear that only his larger specimens were *debruyni*. The smaller specimens evidently belong to a species of the *oculatus–compactus* group.

STEPHENSEN, K., 1912

Stephensen here says: "*Anonyx nugax* is an arctic species, but its distribution cannot be exactly fixed from the literature, as it has earlier often been mixed with the boreal *A. lagena* Kr. (cf. Sars, "Account," vol. 1, p. 686)."

PEARSE, A. S., 1913

Pearse briefly describes and illustrates a new species which he names *Chironesimus multiarticulatus*. The name apparently was chosen because of the large number of articulations in the second antenna, but this is a feature of mature males in this genus. An examination of the type-specimen (to be re-described and illustrated elsewhere by the junior author) has shown that it is a valid species, related to *A. laticoxae* and *A. validus*. It may be distinguished by stout spines on the posterior margin of the sixth segment of peraeopods 3 and 4, lack of constriction in uropod 2, a little-expanded first coxal plate, and setae on the outer edge of the inner ramus of uropod 3.

STEPHENSEN, K., 1913

Stephensen now agrees with previous authors that *A. lagena* Krøyer is a synonym of *A. nugax* (Phipps). The specimens from western Greenland in the Copenhagen Museum that he lists have been re-examined and found to be comprised of several species.

OLDEVIG, H., 1917

Oldevig agrees with Brüggen (1907) and Stappers (1911) that *A. lagena* Krøyer is merely the young of *A. nugax* (Phipps) but goes on to point out that, in the Eisfjord of Spitzbergen, whereas small specimens are found in shallow water, the large specimens (more than 30 mm) were collected only below a depth of 20 m. He ascribes this to a change in depth distribution with age, but it seems likely that the small specimens were *A. sarsi* and/or *A. lilljeborgi*. *Anonyx nugax* was found in the deeper water.

SHOEMAKER, C. R., 1920

Specimens are identified as *Anonyx nugax* (Phipps).

STEPHENSEN, K., 1923

Stephensen reasserts his view that *A. lagena* is a synonym of *A. nugax* (Phipps), and now includes *A. lilljeborgi* in this synonymy, citing the suggestion to that effect made by Stebbing (1894), Norman (1900), and Stappers (1911). He goes on to show, with a map, a graph, and tables, that northern specimens are typically large and have a later breeding season than those from farther south.

However, his specimens from western Greenland that were re-examined have been found to be composed of four species.

BARNARD, K. H., 1925

Two new species, *adversicola* and *rotundatus*, collected in 500–800 fath off the coast of South Africa are described, but not illustrated. These are referred to the genus *Lakota* Holmes, although Barnard points out that this genus differs from *Chironesimus* only in the narrower sixth segment of peraeopod 2 and "that the need for Holmes' genus is extremely doubtful." He also notes that *Chironesimus multiarticulatus* Pearse has a narrow sixth segment in its peraeopod 2 and should be transferred to *Lakota*.

Barnard's type-specimens of the two South African species have been dissected, drawn, and redescribed (to be published elsewhere) by the junior author. They definitely do not belong to the genus *Anonyx* as defined here. With the generic confusion now pervading the *Lysianassidae*, uncertainty still remains as to which genus or genera they belong. Their relations are rather near the genera *Uristes* and *Schisturella*.

SCHELLENBERG, A., 1926

Schellenberg reports the capture of a specimen of *Lakota adversicola* Barnard from deep water near South Africa. He points out that the sixth segment of peraeopod 2 in this species is intermediate between that of *Chironesimus debruyni* as illustrated by Sars (1891) and *Lakota carinata* Holmes, and therefore prefers to refer it to *Chironesimus*. Schellenberg also questions the validity of the genus *Lakota*. He notes some differences, not altogether unimportant in his view, between his specimen and the description of Barnard (1925) and illustrates some of its important structures. Examination of Barnard's holotype has resolved most of these differences, showing that Schellenberg's observations were accurate.

CHEVREUX, E., 1926

Included is *Lakota chelata*, described as new from a single small (4.5 mm) specimen taken off the Lofoten Islands. A re-examination of this specimen has shown it to be a young *A. nugax* (Phipps). The characters deemed to distinguish it are obvious in the illustrations of the young *nugax* presented here.

SHOEMAKER, C. R., 1926

Specimens are identified as *Anonyx nugax* (Phipps).

SCHELLENBERG, A., 1927

Schellenberg follows Stebbing (1906) in his diagnoses of the genus *Anonyx* and of the species *nugax*. He also includes the illustration from Sars (1891).

STEPHENSEN, K., 1928, 1929

In these guides to the Danish and to the North Sea amphipods, in which illustrations are reproduced from Sars (1891), Stephensen shows that he is still a little hesitant about fusing completely *A. lilljeborgi* with *A. nugax*, by distinguishing the former as the "southern form, 11–14 mm in length" occurring in Denmark and southern Norway, and the latter as the "northern form, 40–50 mm in length," occurring in the Arctic.

CECCHINI, C., 1928

Cecchini describes in some detail specimens from Spitzbergen which she calls *Anonyx lagena* Krøyer.

SHOEMAKER, C. R., 1930a

Specimens are identified as *Anonyx nugax* (Phipps).

SHOEMAKER, C. R., 1930b

The head of a mature male of *A. lilljeborgi*, with the antennae and upper lip, is quite recognizably illustrated under the name of *A. nugax*. Shoemaker later correctly identified this species, as shown by notes and illustrations sent to the junior author, and labels in his handwriting with New England specimens, but he still remained puzzled by the variability of several characters.

OLDEVIG, H., 1933

This work is merely a compilation from the literature of information on Swedish amphipods: brief descriptions, keys, Swedish records, and illustrations taken from Sars (1891). Following Stephensen (1928), Oldevig places *A. lilljeborgi* as a synonym of *A. nugax*.

STEPHENSEN, K., 1935

In this publication Stephensen reasserts his conclusion that *A. nugax*, *A. lagena*, and *A. lilljeborgi* are synonyms. He also includes the illustrations and a translation into English of the description of *Lakota chelata* given by Chevreux (1926).

BARNARD, K. H., 1940

Noting the action of Schellenberg (1926), Barnard transfers his *Lakota rotundatus* and *L. adversicola* to *Chironesimus*.

THORSTEINSON, E. D., 1941

Lakota carinata is recorded from the Gulf of Alaska and its first and second peraeopods are illustrated. Three of Thorsteinson's 11 specimens were borrowed from the U.S. National Museum. They belonged to the following three different species: *Anonyx lilljeborgi* (12-mm immature female), *Anonyx ochoticus* (6.5-mm unsexed young), and *Anonyx multiarticulatus* (Pearse) (10-mm mature female).

GURJANOVA, E., 1951

Gurjanova notes that there are seven species in the genus *Anonyx*, which she defines after the diagnosis of Stebbing (1906). Only three are listed as occurring in arctic seas (*A. nugax* (Phipps), *A. lilljeborgi* Boeck, and *A. affinis* Ohlin). *Anonyx lilljeborgi* is accepted as a valid species but little is added that would serve to distinguish it from *A. nugax*. *Anonyx affinis* is described and illustrated from specimens collected in the Japan Sea. However, as discussed above, Ohlin's species cannot be identified with certainty in our opinion and it is questionable if Gurjanova's specimens have been identified correctly. Her determination is presumably based on the urosome keel and on the relatively short inner ramus of uropod 3 found in Ohlin's specimen. However, since these are common features in young individuals as well as in small species of *Anonyx*, they are not sufficient in themselves to distinguish *A. affinis*. She also describes and illustrates specimens from the Japan Sea identified as *A. ampulloides* Bate, but subsequently (1962) has described them as a new species, *A. derjugini*. In addition she also includes summaries of the descriptions and copies of the illustrations of *Chironesimus debruyni* (Hoek), *Chironesimus multiarticulatus* Pearse, and *Lakota chelata* Chevreux.

DUNBAR, M. J., 1954

Specimens are identified as *Anonyx nugax* (Phipps).

BOUSFIELD, E. L., 1956

Specimens are identified as *Anonyx nugax* (Phipps).

BARNARD, J. L., 1958

Barnard chiefly intends to record published nomenclatural transactions, and in most cases does not pretend to accept or reject species in a critical way. He lists five valid species of *Anonyx* (*affinis*, *ampulloides*, *lilljeborgi*, *nugax*, and *wolfendeni*), and 13 doubtful ones. *Anonyx lagena* is treated as a synonym of *A. nugax* on the authority of Stephensen (1923). The genus *Lakota* is placed in the synonymy of *Chironesimus*, as done by Barnard (1940). In the latter genus, six species (*adversicola*, *carinata*, *chelata*, *debruynii*, *multiarticulatus*, and *rotundatus*) are listed, none of them as doubtful.

NAGATA, K., 1960

Nagata records the collection of a number of small specimens which he has identified apparently by means of Stebbing (1888) as *A. ampulloides* Bate. Bate's specimen, however, was found to be a young *A. nugax* by the senior author. Specimens of his species were sent by Nagata to the junior author: after dissection they proved to be quite close to *A. lilljeborgi*, but slightly different from any described species and may require a new name.

BOUSFIELD, E. L., 1962

Specimens are identified as *Anonyx nugax* (Phipps).

BARNARD, J. L., 1962

Barnard lists and illustrates specimens of K. H. Barnard's (1925) *Chironesimus adversicola* and *rotundatus*, the status of which has been discussed previously. He also proposes the fusion of the genera *Tmetonyx* and *Tryphosa*, but, relying on the structure of the first peraeopod and the produced upper lip, he transfers *Tmetonyx nobilis* (Stimpson) to the genus *Chironesimus*.

With the fusion of *Chironesimus* and *Anonyx*, *Tmetonyx nobilis* would be returned to its original designation of *Anonyx nobilis* Stimpson. However, *nobilis* differs in its general appearance and in so many details of its structure that it cannot be referred to *Anonyx* as defined here and therefore should be placed in another genus.

GURJANOVA, E., 1962

In this important work Gurjanova proposes the fusion of the genera *Anonyx* and *Chironesimus* but retains *Lakota* because of a lack of information concerning its structure. In the genus *Anonyx* she then proceeds to describe no less than 25 species and 3 subspecies, 22 as new to science. A number of these also occur in the northwestern Atlantic and their status is discussed in the present work. The results of our observations may be summarized as follows: (1) *Anonyx nugax* (Phipps) is a valid species without recognizable subspecies or varieties; (2) the status of *Anonyx nugax pacificus* should be raised to that of a full species, if our specimens are identified correctly; (3) *A. lilljeborgi* Boeck is a valid species also without recognizable varieties; (4) *A. lilljeborgi lebedi*, which differs from *lilljeborgi* in the possession of spines on peraeopods 3 and 4 and the lack of constriction in uropod 2, is a distinct valid species, related to *A. laticoxae* Gurjanova, *A. multiarticulatus* Pearse, and *A. validus* Gurjanova. (A single 12-mm juvenile male from the Beaufort Sea was discovered in material from the National Museum of Canada, too late for description in the present work.); (5) *A. makarovi*, of which two females (one mature) from the Okhotsk Sea have been found in U.S. National Museum material, is apparently a valid species; (6) *A. affinis* may also be a valid species but is probably not that of Ohlin (1895a); (7) *A. minimus*, which from its eye structure and maxillae appears to be outside the definition of *Anonyx*, actually has a strong resemblance to the newly hatched young of typical *Anonyx* and may have been founded on the young of a larger species. It should be noted, however, that the specimens described are recorded as being 6 mm long, which is considerably longer than the newly hatched young of any species of which we are aware; (8) *A. debruyni* is also without recognizable varieties and sexual differences in the peraeopods. The male of *A. debruyni debruyni* may possibly represent a separate species; (9) *A. debruyni orientalis* probably should also be considered as a distinct species; (10) *A. eous*, of which we have found one 28-mm juvenile male from the Okhotsk Sea in the collections of the U.S. National Museum, is a valid species which, notwithstanding Gurjanova's figures of the mouthparts, has the nodular marginal teeth on the outer lobes of the maxillipeds, and the long proximal seta on the inner lobe of maxilla 2, two characters of generic value in our opinion; the telson with several apical spines per lobe would differ from that of most other species; (11) *A. pavlovski* is apparently also a valid species; a 40-mm juvenile female from the Okhotsk Sea was identified in the collections of the U.S. National Museum; (12) *A. ampulloides* is neither Bate's nor Stebbing's species but the females may belong to *A. compactus*. The males probably represent a separate species; (13) *A. derjugini* represents the species named *A. ampulloides* Bate in Gurjanova (1951); (14) *A. oculatus* is probably identical with the species which Stebbing described under the wrong name of *A. ampulloides* Bate. Gurjanova has also described a number of new species which presumably are valid but have not been found so far in the northwestern Atlantic and may be confined to the northern Pacific.

HURLEY, D. E., 1963

Hurley presents a modification of Stebbing's (1906) diagnosis of the genus. He agrees with Gurjanova (1962) that *Chironesimus* should be a synonym of *Anonyx* but also formally adopts the view that *Lakota* should also be a synonym. Four species of *Anonyx* from the area are described and illustrated.

Hurley's *A. carinatus* is obviously *A. lilljeborgi* as described here, but his *A. lilljeborgii* (?) is apparently a distinct valid species. He has probably been misled by Gurjanova (1962) into considering *A. lilljeborgi* to have an unconstricted inner ramus of uropod 2, whereas the reverse is true. This character, plus the hairy distal segment of the maxilliped palp, distinguishes his *A. lilljeborgii* (?) from the true *A. lilljeborgi* Boeck, and relates it to *A. multiarticulatus* (Pearse). From the latter it differs in the linguiform upper lip, and especially in the unique long spine on the hind edge of segment 6 of peraeopod 3 (Hurley's p.1).

Anonyx dorotheae, which is described from small (3 mm), probably immature specimens, belongs to the genus *Schisturella* Norman, 1900. The small coxal plate on peraeopod 1, the long aesthetascs at the base of the flagellum of antenna 1, the armature of the maxilliped outer lobe, the armature of the rami of uropod 3 and perhaps the broad sinus above the upper lip, all these add up to sufficient reasons for excluding this species from the genus *Anonyx*. Hurley (personal communication) has agreed with this change.

The fourth species, *Anonyx adoxus*, also raises some doubts as to its generic position. There is also a broad sinus above the upper lip (artefact?), the first flagellar segment of antenna 1 also has several long aesthetascs, the outer lobe of maxilla 1 has fewer than 11 spines and the proximal two are not distinctly separated from the others, the palm of peraeopod 1 has no acute crowded denticles and is marked by only one strong spine and what is apparently a seta, the dactyl of peraeopod 3 (Hurley's p. 1) is uncurved, the distal spines of peraeopods 3, 5, and 7 (Hurley's p. 1, 3, and 5) are unusually long and strong, the first coxal plate is markedly unexpanded and distally rounded, the outer ramus of uropod 3 has unusually strong spines and a short distal segment, and the inner ramus is spineless, and the margins of the third metasome lateral plate are remarkably evenly rounded; all these characters distinguish *A. adoxus* from all the species of *Anonyx* which we have examined. However, some of these differences may not stand after examination of actual specimens: the status of the species is therefore left in abeyance.

BRUNEL, P., 1964

An illustration of *Anonyx compactus* (reproduced as Fig. 50A of the present work) is given and identified as *A. oculatus*, as we were inclined to think at that time.

SHOEMAKER, C. R., 1964

In this posthumous paper, Shoemaker describes the new genus and species *Kyska dalli* from specimens taken in the North Pacific, near the western Aleutian Islands. He observes that this genus is identical to the genus *Anonyx*, from which it differs only in "the comparative shortness of the antennae, the lack of calceoli in the male, and the possession of chelate gnathopod 1 in both sexes." We note, firstly, that the antennae of *Kyska* have almost the same relative lengths as *Anonyx laticoxae* and other species described by Gurjanova (1962), and are dependent on maturity in any event. Secondly, we fail to see how it is possible to assert that the males lack calceoli if none of those examined were mature, calceoli being the very criterion of maturity in the male, and short antennae with crowded segments being furthermore characteristic of submature males. Thirdly, the chelate condition of the first peraeopod departs no more radically from the same limb in other *Anonyx* species than do both peraeopods 1 and 2 of *Chironesimus*. The other characters of *Kyska*, especially the mouthparts, are so similar to those of *Anonyx* that we would propose its synonymy with *Anonyx*, were it not for the absence of transitional states between the chelate condition of peraeopod 1 of *Kyska* and the subchelate condition of that of many *Anonyx* species. This appears to be the only obvious character distinguishing these genera, although the distal spur of peraeopods 3–4, the structure of uropod 2 and the projection of the upper lip are not described or illustrated accurately by Shoemaker. Uropod 2 appears to be unconstricted, as far as the illustration shows. In the spectrum of specific characters used in the genus *Anonyx*, therefore, *Kyska* seems to stand at the opposite end from that occupied by the *Chironesimus* group, its characters being the opposite of those listed for the latter group in the discussion of generic synonymy given above. The single spine defining the palm of peraeopod 1, apparently unique in the genus, is worth noting in this respect.

KUZNETSOV, V. V., 1964

In this posthumous work, Kuznetsov (who died in 1961) devotes 19 pages to "*Anonyx nugax*," which he studied from 1947 to 1951 in the Barents and White seas. The author gives extensive quantitative data on regional, seasonal, and daily variations of abundance as related to depth and lunar phases, on size-frequency distributions and on length–weight relations. Trap catches were very much larger at night than in the day, and were largest in winter months when they were clearly related to the length of night from February to April. Kuznetsov's larger size modes (15–20 and 34–36 mm) indicate that he was probably dealing with at least two species,

presumably *A. sarsi* and *A. nugax*, although no information on maturity stages is apparently given in the table. The largest individuals were 24 mm long in the Barents Sea and 46 mm in the White Sea: one may infer from this that *sarsi* is the largest species in the southern Barents Sea, but that *nugax* occurs in the colder White Sea. It is most unfortunate that this enormous work of counting the reported hundreds of thousands of specimens and of measuring hundreds of individuals is left almost worthless by the taxonomic lumping of the species which prevailed at the time.

KUDRJASCHOV, V. A., 1965

Kudrjaschov describes two new species of *Anonyx* collected in the Sea of Okhotsk as follows. *Anonyx epistomicus*: the single specimen which was 13 mm long has a constricted uropod 2 and a large posteriorly projecting keel on urosome segment 1; the telson lobes bear three terminal spines and two conspicuous spines define the palm or peraeopod 2. The most distinct character, however, is the produced epistome which overhangs the upper lip and in which this species would differ from all other species in the genus. *Anonyx volkovi*: this was described from two small (up to 5 mm) specimens and is without any important feature that could serve to distinguish it from the young of the many *Anonyx* species found in the Okhotsk Sea.

Kudrjaschov also describes a new genus *Pseudoanonyx* which is considered to be closely related to *Anonyx*. It lacks eyes, the spurs on segment 6 of peraeopods 3–4, and apparently the palm-defining spines on peraeopod 1, but there are three spines near the palmar angle. In addition, the terminal segment of the maxilliped palp is large and thick.

SCARRATT, D. J., 1965

Weakened lobsters are described as being attacked and partially consumed by *Anonyx* sp., specimens of which were sent to the junior author and identified as *Anonyx sarsi* n.sp.

SHAVE, P.A., 1966

Sand fleas which quickly consume the bait in lobster traps in the Cape Cod area are identified as the lysianassid amphipods *Orchomenella* and *Anonyx* sp.

STEELE, D. H., 1967

A large species (*Anonyx bispinosus*) from the Barents Sea with a completely constricted inner ramus on uropod 2 is described as new to science and illustrated in detail.

DISCUSSION

SYSTEMATICS

The literature on the genus *Anonyx* is full of poor and incomplete descriptions and errors of identification caused by a failure to refer to the type-specimens even when they were available. Also, there has been too great a reliance on characters such as the relative length of the segments of peraeopod 1 and the rami of the uropods, which lead to similar errors unless there is an understanding of how these characters vary as the animal grows. This exists even in quite recent publications. It is hoped that the present publication will encourage the study of variations with size and their inclusion as an integral part of future work. If similar size-variations occur in other genera, many species and possibly even genera may turn out to be synonyms of older species.

On the other hand, we are reluctant to accept a developing trend toward fusion of large lysianassid genera, such as Barnard's (1962) fusion of *Tmetonyx* and *Tryphosa*, when no attempt is apparently being made to follow on the productive footsteps of Boeck, Sars, and Stebbing, in describing and illustrating mouthparts in detail and in striving to discover new generic and specific

characters. Such action, supported by re-examination of type-specimens, is likely to establish on a firmer basis the generic and specific boundaries which were set up with so much insight and thoroughness by the pioneers just named. In our opinion, the present study demonstrates that an abundance of important and hitherto unutilized morphological features may be put to use to re-define and probably break up (rather than fuse) along new boundaries many large genera which have become blurred by an over-abundance of newly, and often insufficiently, described species. Fusion of small and poorly justified genera may of course result from such action, as in the case of *Lakota* and *Chironesimus* which were fused with *Anonyx*, and the nomenclature may be enhanced thereby.

It appears to us that generic characters based on the length and number of segments of the two antennae and on the first two peraeopods will either have to be abandoned, made much more accurate, or used only at the species level. As Barnard (1962) rightly points out upon fusing *Tmetonyx* with *Tryphosa*, the degree of subchelation of peraeopod 1 varies in an almost continuous manner among the species, and other characters recombine in endless variety. However, the conclusion from this, as well as from the work of several authors on *Gammarus*, that of Mills (1964, 1967) on *Ampelisca*, and our own research, is that (1) characters subject to variable gradients of allometric growth which affect shapes and proportions are unsuitable at the generic level and often also at the specific level; and (2) better characters of a meristic or qualitative nature can be found in the armature and fine structure of various limb segments, including mouthparts. The challenge now is at the same time to restore or destroy the value of the former by resorting to morphometric methods, and to discover more of the latter. We agree with Hurley (1963), therefore, that there is an urgent need for revisions in the Lysianassidae, and we would even add that such work should now have priority over new faunistic surveys and descriptions of new species: whatever the value of the latter to reveal full generic variability, nothing but nomenclatural anarchy will ensue if half of them are referred to wrong genera, meaningless names, or new genera which become synonyms on the next day.

Anonyx appears to be a rapidly evolving genus and several species are presumably closely related. Many of them are scavengers or even predators of weakened animals and may often be collected in large numbers with bait. The mouthparts are strong and quite stable throughout the genus. All of the species look alike superficially and structural differentiation between them involves mainly the second uropod, the second peraeopod, and the presence or absence of spines on peraeopods 3 and 4. Equally important, however, are differences in size at maturity, which is the main factor separating several species.

Zoogeography

The distribution of the eight North Atlantic species is summarized and compared in quantitative terms in Table IX. Although these figures obviously

TABLE IX. Numbers of specimens of the eight species of *Anonyx* in the material examined according to geographical areas, with number of samples given in parentheses.

Species	Northwest Atlantic: Arctic Ocean to Labrador (incl. W Greenland)	Northwest Atlantic: Gulf of St. Lawrence to Delaware	Alaska & North Pacific	Northeastern Atlantic and European Arctic (incl. E Greenland)	Total
A. nugax	634(126)	233(42)	130(10)	155(36)	1152(214)
A. lilljeborgi	322(32)	1225(161)	1(1)	70(14)	1618(208)
A. sarsi	315(62)	1026(116)	32(5)	321(16)	1694(199)
A. pacificus	65(26)	174(50)	61(2)	–	300(78)
A. laticoxae	349(34)	1(1)	221(9)	7(4)	588(48)
A. ochoticus	37(11)	120(17)	4(3)	–	161(31)
A. compactus	4(2)	35(20)	2(1)	–	41(23)
A. debruyni	–	30(12)	–	1(1)	31(13)
Total	1726(293)	2844(419)	451(31)	565(72)	5585(814)

reflect both the distribution of past surveys of the fauna and our selection of a main study area, they have some comparative value because of the relative lack of bias presumably exercised in the sampling of the different species. The data reveal three obvious trends. Firstly, the three most abundant and most common species, *A. nugax*, *A. lilljeborgi*, and *A. sarsi*, which account for about three-quarters of the specimens as well as of the samples, are the only three which are unquestionably circumpolar in distribution. Secondly, only two species, *A. nugax* and *A. laticoxae*, are decidedly more abundant and frequent in the Arctic than farther to the south, *A. laticoxae* being overwhelmingly so. Thirdly, three species, *A. pacificus*, *A. ochoticus*, and *A. compactus*, are not recorded from the northeastern Atlantic and European Arctic. Their distribution also exhibits the apparent paradox (discussed more fully below) of a southern predominance in the coldest waters (e.g. the intermediate cold layer in the Gulf of St. Lawrence) and a reduced abundance and frequency in the Arctic. *Anonyx laticoxae* has a similar mainly western distribution, but it differs in its occurrence to the east (although this needs confirmation), and its scarcity to the south.

As defined here, *Anonyx* contains between 25 and 30 species, almost all of which are found in the northern Pacific. These show several evolutionary trends, but with Hurley (1963) one may tentatively subdivide the genus into three groups on the basis of the degree of constriction of the inner ramus of uropod 2: complete, moderate, and absent.

Those with completely constricted uropod rami are especially prevalent in the Pacific, which may be presumed to be their center of origin. The northwestern Atlantic has only two of these species, *A. ochoticus* and *A. compactus*, apparently inhabiting mainly the coldest water masses (e.g. the intermediate

layer of the Gulf of St. Lawrence). The northeastern Atlantic has no records of species with this type of structure, except for the new species just described from the Barents Sea (Steele, 1967), and the small specimens recorded as *C. debruyni* by Stappers (1911), whatever they turn out to be. When the extensive collections available for the northeastern Atlantic are re-evaluated, this picture may change. It appears now, however, that the species with completely constricted uropods have originated in the cold regions of the northern Pacific and have spread eastward and perhaps also westward to reach the fringes of the Atlantic, where they remain in very cold water.

A similar pattern is evident in those species with unconstricted rami. Most are confined to the Pacific and the one Atlantic species, *A. laticoxae*, has been found only as far east as western Greenland and as far west as Franz Joseph Land and Spitzbergen.

A different situation prevails in those species with moderately constricted rami. Five of the eight species of the northwestern Atlantic belong to this group and only one, *A. pacificus*, does not occur in the northeastern Atlantic. The distribution of *A. pacificus* is similar to that of other so-called Pacific–west Atlantic species ably discussed by Nesis (1962), except that it is scarce instead of absent in the Canadian Arctic Archipelago. With those species, *pacificus* shares five zoogeographical features: (1) it is apparently absent from the northeastern Atlantic and European Arctic; (2) it has many more relatives in the North Pacific than in the North Atlantic or Arctic; (3) it lives in permanently cold (−1 to 2 C) waters along the Canadian Atlantic coasts (although it may occur in warmer water); (4) it occurs therein as a dominant species; but (5) its abundance in the Canadian Arctic is reduced. The North Pacific origin and migration path of a species with such a distribution is nowadays generally agreed upon (Nesis, 1962, and papers cited therein). The enigmatic feature of its distribution rather resides in its apparent scarcity in the Canadian Arctic, as contrasted with its relative abundance in cold water in the south. The explanations recorded by Nesis for species with nonpelagic development amount to making the two suppositions that, from the time of their original warmer-water adaptation in the North Pacific, they (*a*) migrated eastward during the "Littorina" period of warmer arctic temperatures after the last glaciation; and (*b*)′ were later eliminated from the Arctic by their failure to adapt to the subsequent cooling within the short time when they had been there. Inherent to this explanation are the slightly higher temperatures (0–4 C), available in summer (for breeding?) to the surviving southern populations within or close to their water mass, than the negative temperatures which had formerly killed the species in the Arctic.

Anonyx pacificus is here recognized as the closest relative of *A. nugax* in the North Atlantic and Canadian Arctic. Its more restricted geographical distribution indicates that it is *pacificus* which must have originated from a stock of *nugax*, presumably during the Pleistocene. Their distribution patterns, where they overlap geographically, are puzzling, and may give clues to this origin. Among the large species, *A. nugax* is dominant over *pacificus* (and

sarsi and *laticoxae*) in the Canadian Arctic, whereas in the Gulf of St. Lawrence (and probably on the Newfoundland and Nova Scotian banks) it is dominant in the bathyal Laurentian Channel (2–5 C), and (with *sarsi*) in the surface layer, at least in the north (about 3–14 C in summer), *pacificus* being dominant in the coldest (–1 to 2 C) intermediate water layer. These distribution patterns are probably best explained by a delicate competitive adjustment which might have arisen as follows. *Anonyx pacificus* may have originated in the cold water masses of the North Pacific from a Pleistocene stock of the eurythermic *nugax* which was denied access to the Arctic Ocean by the Bering Strait land bridge. After the reflooding of Bering Strait, it may have invaded the Arctic Ocean with the northward-flowing current and emigrated as far as Baffin Island and the Nova Scotian Shelf. In the Arctic, it may always have been out-competed, in its quest for limited resources, by the more ancient resident of these areas, *nugax*, which is now circumpolar in distribution. But further south, it succeeded in out-competing *nugax* in the permanently cold water in which it may have originated. Other species of Pacific origin discussed by Nesis (1962), such as *Echinarachnius parma* Lamarck, whose eurythermy enabled them to invade so successfully the shallow boreal water layer, did so in the absence of any closely related competitor. *Anonyx pacificus*, for its part, probably had two competitors, *sarsi* and *nugax*.

Anonyx lilljeborgi and *A. sarsi* have more decidedly southern horizontal distributions, and tolerances of higher temperatures than *A. nugax*. They may have had a similar origin to that of *pacificus* and dispersed more rapidly so as to become circumpolar, or possibly evolved in an earlier period of isolation and have had longer for their dispersal. The fact that they diverge more from *A. nugax* in their morphology gives added weight to the latter hypothesis. On the other hand, it is possible that they may have originated in the Atlantic and dispersed from there.

Anonyx debruyni is a species of deeper water of which little is known. However, its structure other than that of its second uropod is quite different from the other members of this group and it probably has a more ancient origin. The long first flagellar segment of antenna 1, some details of the mouthparts, the unexpanded first coxal plate, the short palm and hind-edge spines of segment 6 of peraeopod 1, the long palm and finger of peraeopod 2, and its relatively small size at maturity, are reminiscent of some species in the group with completely constricted uropods, especially those in the *oculatus–compactus* group.

It should be emphasized that the patterns of distribution discussed above may change when more of the collections from the northeastern Atlantic are re-examined. Also, that the status of a number of the Pacific species is uncertain and much further study remains to be done on these forms.

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REFERENCES

BARNARD, J. L. 1958. Index to the families, genera, and species of the gammaridean Amphipoda (Crustacea). Occasional Papers Allan Hancock Found., **19**: 1–145.

1962. South Atlantic abyssal amphipods collected by R.V. Vema. *In* Abyssal Crustacea. Vema Res. Ser., **1**: 1–78.

BARNARD, K. H. 1925. Contributions to the crustacean fauna of South Africa. No. 8. Further additions to the list of Amphipoda. Ann. S. African Museum, **20**(5): 319–380.

1940. Contributions to the crustacean fauna of South Africa. No. 12. Further additions to the Tanaidacea, Isopoda and Amphipoda, together with keys for the identification of hitherto recorded marine and freshwater species. Ibid., **32**(5): 381–543.

BATE, C. S. 1858 On some new genera and species of Crustacea Amphipoda. Ann. Mag. Nat. Hist., (3)**1**: 361–362.

1862. Catalogue of the specimens of amphipodous Crustacea in the collection of the British Museum. British Museum (Nat. Hist.), London. 399 p.

BATE, C. S., AND J. O. WESTWOOD. 1861. A history of the British sessile-eyed Crustacea, Vol. 1. London. p. 1–144. (Parts I–IV covering the Lysianassidae in the first 144 pages were issued from October to December 1861, according to Stebbing, 1888.)

BELL, T. 1855. An account of the Crustacea. *In* E. Belcher [ed.] The last of the arctic voyages; being a narrative of the expedition in H.M.S. Assistance, under the command of Captain Sir Edward Belcher, C.B., in search of Sir John Franklin during the years 1852–1853–1854. Vol. 2. Lowell Reeve, London. p. 404–407.

BLANC, H. 1884. Die Amphipoden der Kieler Bucht nebst einer histologischen Darstellung der "Calceoli". Nova Acta Leopoldina, **47**(2): 37–96.

BOECK, A. 1870. Crustacea amphipoda borealia et arctica. Vidensk. Selsk. Forhandl., 1870: 81–280.
1872, 1876. De skandinaviske og arktiske Amphipoder. 713 p. Christiania.

BOUSFIELD, E. L. 1956. Studies on the shore fauna of the St. Lawrence estuary and Gaspé coast. Natl. Museum Canada Bull., **136**: 95–101.
1962. Studies on littoral marine arthropods from the Bay of Fundy region. Ibid., **183**: 42–62.

BRÜGGEN, E. VON DER. 1907. Zoologische Ergebnisse der russischen Expeditionen nach Spitzbergen. Amphipoda. Ann. Museum Zool. Acad. Imp. Sci. St. Pétersbourg, **11**(1906): 214–245.

BRUNEL, P. 1964. Recherches sur les invertébrés de fond à la Station de Biologie marine. Actualités Marines, **7**(3): 3–8.

BRUZELIUS, R. M. 1859. Bidrag till kännedomen om Skandinaviens Amphipoda Gammaridea. Kgl. Svenska Vetenskapsakad. Handl., **3**(1): 1–104.

BUCHHOLZ, R. 1874. Crustaceen. *In* Die zweite Deutschen Nordpolarfahrt in den Jahren 1869 und 1870 unter Führung der Kapitän Karl Koldewey. Wiss. Ergeb. Zool., **2**(8): 262–399.

CECCHINI, C. 1928. Gli Anfipodi del R. Museo Zoologico di Firenze. Fam. Lysianassidae – Gen. *Pseudalibrotus, Lysianassa, Aristias, Anonyx, Socarnes*. Atti. Accad. Fisiocrit., Siena, (10)**3**: 113–128.

CHEVREUX, E. 1926. Diagnoses d'Amphipodes nouveaux provenant des campagnes de la "Princesse-Alice" dans l'Atlantique et dans l'océan arctique. Bull. Inst. Océanog. Monaco, **23**(475): 1–12.

DUNBAR, M. J. 1954. The amphipod Crustacea of Ungava Bay, Canadian eastern arctic. J. Fish. Res. Bd. Canada, **11**(6): 709–798.

FABRICIUS, J. C. 1781. Species insectorum exhibentes eorum differentias specificas, synonyma Auctorum, loca natalia, metamorphosim adjectis observationibus descriptionibus. Tom 1. Hamburg.

GOËS, A. T. 1866. Crustacea amphipoda maris Spetsbergiam alluentis, cum speciebus aliis arcticis enumerat. Öfversigt Kgl. Vetenskapsakad. Förhandl., **1865**(8): 517–536.

GORDON, I. 1960. On a *Stygiomysis* from the West Indies, with a note on *Spelaeogriphus* (Crustacea, Peracarida). Bull. Brit. Museum (Nat. Hist.), **6**(5): 285–324.

GRIMM, O. 1880. Beitrag zur Kenntniss einiger blinden Amphipoden des Kaspisee. Arch. Naturgesch., **46**(1): 117–126. (Transl. Ann. Mag. Nat. Hist., February 1880.)

GURJANOVA, E. 1951. Bokoplavy morei SSSR i sopredelnykh vod (Amphipoda-Gammaridea). Opred. Faune SSSR, Akad. Nauk. SSSR, **41**: 1029 p.
1962. Bokoplavy severnoi chasti Tikhogo Okeana (Amphipoda-Gammaridea). Chast. 1. Ibid., **74**: 440 p.

HANSEN, H. J. 1887. Malacostraca marina Groenlandiae occidentalis. Översigt. over det vestlige Grønlands Fauna af malakostrake Havkrebsdyr. Vidensk. Medd. Naturhist. Foren. Kjøbenhaven, 1887: 3–226.

HELLER, C. 1875. Die Crustaceen, Pycnogoniden und Tunicaten der K. K. Österr.-Ungar. Nordpol-Expedition. Denkschr. Akad. Wiss. Wien, Math.-Natuurw. Klg., **35**: 25–44.

HOEK, P. P. C. 1882. Die Crustaceen gesammelt waehrend der Fahrten des "Willem Barents" in den Jahren 1878 und 1879. Niederl. Arch. Zool. Suppl.-Bd,. **1**(3): 1–75.

HOLMES, S. J. 1904. On some new or imperfectly known species of West American Crustacea. Proc. Calif. Acad. Sci., (3)**3**: 307–330.
1905. The Amphipoda of southern New England. Bull. U.S. Bur. Fish., **24**(1904): 457–529.
1908. The Amphipoda collected by the U.S. Bureau of Fisheries steamer "Albatross" off the west coast of North America, in 1903 and 1904, with descriptions of a new family and several new genera and species. Proc. U.S. Natl. Museum, **35**(1654): 489–543.

HURLEY, D. E. 1963. Amphipoda of the family Lysianassidae from the west coast of North and Central America. Occasional Papers Allan Hancock Found., **25**: 1–160.

KRØYER, H. N. 1838a. Grønlands Amfipoder. Vidensk. Selsk. Naturv. Math. Afhandl., 7: 229–326.

1838b. Conspectus crustaceorum Groenlandiae. Naturhist. Tidsskr., (1)**2**: 249–261.

1842. Nye nordiske Slaegter og Arter af Amfipodernes Orden, henhørende til Familien Gammarina. Ibid., (1)**4**: 141–166.

1845. Karcinologiske Bidrag. Ibid., (2)**1**: 453–637.

1846. Karcinologiske Bidrag. Ibid., (2)**2**: 1–211.

KRØYER, H. N.? 1846? Crustacés. *In* Paul Gaimard [ed.] Voyages de la commission scientifique du Nord; en Scandinavie, en Laponie, au Spitzberg et aux Ferö, pendant les années 1838–1840, sur la corvette la Recherche, commandée par M. Fabvre. Atlas. Paris.

KUDRJASCHOV, V. A. 1965. Novye vidy bokoplavov semeistva Lysianassidae (Amphipoda, Gammaridea) iz Okhotskovo moria. [New amphipod species of the family Lysianassidae (Amphipoda, Gammaridea) from the Okhotsk Sea.] Zool. Zh., **44**(4): 513–520.

KUZNETSOV, V. V. 1964. Biologiya massovykh i naibolee obychnykh vidov rakoobraznykh Barentseva i Belovo morei. [Mass-biology of the most common crustaceans of the Barents and White seas.] Acad. Sci. USSR, Moscow–Leningrad. 242 p.

LATREILLE, P. A. 1829. Crustacés, Arachnides et partie des Insectes. *In* G. Cuvier [ed.] Le Règne animal....., n. ed., Vol. 4. Paris.

LAVERACK, M. S. 1964. The antennular sense organs of *Panulirus argus*. Comp. Biochem. Physiol., **13**(4): 301–321.

LEYDIG, F. 1878. Ueber Amphipoden und Isopoden. Anatomische und zoologische Bemerkungen. Zeitschr. Wiss. Zool., **30**(suppl.): 225–274.

LILLJEBORG, W. 1865. On the *Lysianassa magellanica* H. Milne Edwards, and on the Crustacea of the suborder Amphipoda and subfamily *Lysianassina* found on the coast of Sweden and Norway. Nova Acta Reg. Soc. Sci. Uppsaliensis, (3)**6**: 1–38.

LOCKINGTON, W. N. 1877. Descriptions of seventeen new species of Crustacea. Proc. Calif. Acad. Sci., **7**: 41–48.

MIERS, E. J. 1877a. List of the species of Crustacea collected by the Rev. A. E. Eaton at Spitzbergen in the summer of 1873, with their localities and notes. Ann. Mag. Nat. Hist., (4)**19**: 131–140.

1877b. Report on the Crustacea collected by the naturalists of the Arctic Expedition in 1875–76. Ibid., (4)**20**: 52–66, 96–110.

MILLS, E. L. 1964. *Ampelisca abdita*, a new amphipod crustacean from eastern North America. Canadian J. Zool., **42**(4): 559–575.

1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Bd. Canada, **24**(2): 305–355.

MILNE-EDWARDS, H. 1840. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Vol. 3. Boret, Paris. 638 p.

NAGATA, K. 1960. Preliminary notes on benthic gammaridean Amphipoda from the *Zostera* region of Mihara Bay, Seto Inland Sea, Japan. Publ. Seto Marine Biol. Lab., **8**(1): 163–182.

NESIS, K. N. 1962. Tikhookeanskie elementy v bentose severo-zapadnoi Atlantiki. [Pacific elements in Northwest Atlantic benthos.] *In* Yu. Yu. Marti [ed.] Sovetskie rybokhozyaistvennye issledovaniya v severozapadnoi chasti Atlanticheskogo okeana [Soviet Fisheries Investigations in the Northwest Atlantic.] VNIRO-PINRO, Moscow. (English translation, 1963, by Israel Program for Scientific Translations.)

NORMAN, A. M. 1900. British Amphipoda: Fam. Lysianassidae (concluded). Ann. Mag. Nat. Hist., (7)**5**: 196–214.

OHLIN, A. 1895a. Bidrag till kännedomen om malakostrakfaunan i Baffin Bay och Smith Sound. Acta Univ. Lund., **31**: i–xxii, 1–72.

1895b. Additional notes to my paper: "Bidrag till kännedomen om malakostrakfaunan i Baffin Bay och Smith Sound." Zool. Anz., **18**: 485–487.

OLDEVIG, H. 1917. Die Amphipoden, Isopoden und Cumaceen des Eisfjord. *In* Zool. Ergeb. Schwed. Expedition Spitzbergen 1908, Teil 2:8. Kgl. Svenska Vetenskapsakad. Handl., **54**(8): 1–56.
1933. Sveriges Amphipoder. Medd. Göteborgs Museum Zool. Avdeln., **62** [Göteborgs Vetensk. Vitterhets-Samhälles Handl., Femte Följden, (B) **3**(4)]: 1–282.

PARRY, W. E. 1824. Journal of a second voyage for the discovery of a north-west passage from the Atlantic to the Pacific; performed in the years 1821–22–23, in his Majesty's ships Fury and Hecla, under the orders of Captain William Edward Parry, R.N., F.R.S. and Commander of the Expedition. J. Murray, London. 571 p.

PEARSE, A. S. 1913. Notes on a small collection of amphipods from the Pribilof Islands, with descriptions of new species. Proc. U.S. Natl. Museum, **45**(1998): 571–573.

PHIPPS, C. J. 1774. Appendix: natural history. *In* C. J. Phipps [ed.] A voyage towards the North Pole, undertaken by his Majesty's command, 1773. J. Nourse, London. p. 191–193.

ROSS, J. C. 1826. Appendix: Zoology. *In* W. E. Parry [ed.] Journal of a third voyage for the discovery of a north-west passage from the Atlantic to the Pacific; performed in the years 1824–25, in his Majesty's ships Hecla and Fury, under the orders of Captain William Edward Parry, R. N., F.R.S. J. Murray, London. p. 91–120.
1828. Appendix: Zoology. *In* W. E. Parry [ed.] Narrative of an attempt to reach the North Pole, in boats fitted for the purpose, and attached to his Majesty's ship Hecla, in the year MDCCCXXVII, under the command of Captain William Edward Parry, R.N., F.R.S. J. Murray, London. p. 189–206.
1835. Appendix: Marine invertebrate animals. *In* J. Ross [ed.] Narrative of a second voyage in search of a north-west passage and of a residence in the Arctic regions during the years 1829, 1830, 1831, 1832, 1833. Vol. 2. W. Webster, London. p. lxxxi–xcviii.

SABINE, E. 1824. An account of the animals seen by the late northern expedition whilst within the Arctic Circle. *In* W. E. Parry [ed.] Journal of a voyage for the discovery of a north-west passage from the Atlantic to the Pacific; performed in the years 1819–20 in his Majesty's ships Hecla and Griper under the orders of William Edward Parry, R.N., F.R.S. J. Murray, London. p. ccxix–ccxxxix.

SARS, G. O. 1871. Beskrivelse af de paa Fregatten Josephines expedition funde Cumaceer. Kgl. Svenska Vetenskapsakad. Handl., **9**(13): 1–57.
1885. Crustacea, I. Description of new or imperfectly known species. Norske Nordhavs-Exped. 1876–1878, Zoology, **6**(14): 1–280.
1891. Amphipoda. An account of the Crustacea of Norway. Vol. 1, Pt. 4. Pl. 25–32. Cammermeyer, Christiania. p. 69–92.
1895. Amphipoda. An account of the Crustacea of Norway. Vol. 4, suppl. part (appendix). Cammermeyer, Christiania. p. 673–711.

SCARRATT, D. J. 1965. Predation on lobsters (*Homarus americanus*) by *Anonyx* sp. (Crustacea, Amphipoda). J. Fish. Res. Bd. Canada, **22**(4): 1103–1104.

SCHELLENBERG, A. 1926. Amphipoda 3: Die Gammariden der Deutschen Tiefsee-Expedition. Wiss. Ergebn. Deut. Tiefsee-Expedition "Valdivia" 1898–99, **23**(5): 193–244.
1927. Amphipoda des nordischen Plankton. Nord. Plankton, **3**(6): 589–722.

SCHNEIDER, J. S. 1884. Undersøgelser af dyrelivet i de arktiske fjorde. II. Crustacea og Pycnogonida indsamlede i Kvaenangsfjorden 1881. Tromsø. Museum Aarshefter, **7**: 56–134.

SEGERSTRALE, S. G. 1937. Zur Morphologie und Biologie des Amphipoden *Pontoporeia affinis*, nebst einer Revision der *Pontoporeia*-Systematik. Comm. Biol. Soc. Sci. Fennica, **7**(1): 1–28.

SHAVE, P. A. 1966. Sand fleas are pests to our lobstermen. Falmouth Gazette (Mass.), Nov. 25. p. 6.

SHOEMAKER, C. R. 1920. The amphipods of the Canadian Arctic Expedition, 1913–18. Rept. Canadian Arctic Expedition, 1913–18, **7**(E): 1–30.
1926. Report on the marine amphipods collected in Hudson and James Bays by Frits Johansen in the summer of 1920. *In* Results of the Hudson Bay Expedition in 1920. Contrib. Canadian Biol. Fish., **3**(1): 1–11.
1930a. The lysianassid amphipod crustaceans of Newfoundland, Nova Scotia and New Brunswick in the USNM. Proc. U.S. Natl. Museum, **77**(2827): 1–19.
1930b. The Amphipoda of the Cheticamp Expedition of 1917. Contrib. Canadian Biol. Fish., N. S., **5**(10): 221–359.
1964. Seven new amphipods from the West Coast of North America with notes on some unusual species. Proc. U.S. Natl. Museum, **115**(3489): 391–430.

STAPPERS, L. 1911. Crustacés Malacostracés. Duc d'Orléans, Campagne Arctique de 1907. Bruxelles. p. 1–152.

STEBBING, T. R. R. 1876. Amphipodous crustaceans. On the genera *Hyale*, and *Anonyx* and a new species of *Probolium*. Ann. Mag. Nat. Hist., (4)**17**(101): 337–346.

1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–1876. Rept. Sci. Res. Challenger, Zool., **29**: 1–1690.

1894. The Amphipoda collected during the voyages of the Willem Barents in the arctic seas in the years 1880–84. Bijdr. Dierk., **17**: 1–47.

1906. Amphipoda. I. Gammaridea. Das Tierreich, **21**: 1–806.

STEELE, D. H. MS, 1961. Studies in the marine Amphipoda of eastern and northeastern Canada. Ph.D. Thesis. McGill University, Marine Sciences Centre, Montreal, Que.

1967. A new species of the genus *Anonyx* (Crustacea, Amphipoda) from the Barents Sea. Crustaceana, **13**(3): 257–264.

STEPHENSEN, K. 1912. Report on the Malacostraca, Pycnogonida and some Entomostraca collected by the Danmark Expedition to north-east Greenland. Medd. Grønl., **45**(11): 501–630.

1913. Grønlands Krebsdyr og Pycnogonider (Conspectus crustaceorum et pycnogonidorum Groenlandiae). Ibid., **22**(1): 1–479.

1923. Crustacea Malacostraca V (Amphipoda I). Danish Ingolf-Expedition, 3(8): 1–100.

1928. Storkrebs. II. Ringkrebs i tanglopper (Anfipoder). Danmarks Fauna, **32**: 1–399.

1929. Amphipoda. Tierw. Nord Ostsee, X(f) (Lief. 14): 1–188.

1935. The Amphipoda of N. Norway and Spitsbergen with adjacent waters. Tromsø Museums Skrifter, **3**(1): 1–140.

STIMPSON, W. 1853. Synopsis of the marine Invertebrata of Grand Manan, or the region round the Bay of Fundy, New Brunswick. Smithsonian Contrib. Knowledge, **6**: 1–67.

TATTERSALL, W. M. 1909. Amphipoda and Isopoda, with descriptions of two new species. *In* R. N. Wolfenden [ed.] Scientific and biological researches in the North Atlantic, conducted by the author on his yachts "The Walwin" and the "Silver Belle". Memoirs Challenger Soc., **1**: 210–219.

TATTERSALL, W. M., AND O. S. TATTERSALL. 1951. The British Mysidacea. Ray Soc. Publ., London, **136**: viii + 460 p.

THORSTEINSON, E. D. 1941. New or noteworthy amphipods from the North Pacific Coast. Univ. Wash. Publ. Oceanog., **4**(2): 50–96.

VOSSELER, J. 1889. Amphipoden und Isopoden von Spitzbergen. *In* W. Kükenthal [ed.] Beiträge zur Fauna Spitzbergens. Arch. Naturgesch., **55**: 151–162.

NOTES

Commercial Redfish and Flatfish (Flounder) Oils: Comparative Features of Fatty Acid Composition[1]

Production of marine oils in Canada is at present based largely on whole-body reduction of herring (clupeids). The fatty acid composition of herring oils has recently been reported in some detail (Ackman and Eaton, 1966a; Ackman et al., 1967). Oils of diverse origin formerly produced are mentioned by Bailey (1952) and a number of these are still of some commercial significance. On the Atlantic coast there is commercial production from filleting plant offal of two additional oils, from redfish and from flatfish (usually flounder or sole). A substantial part of the commercial redfish oil will come from muscle scrap (~3% fat), but flounder muscle (~1% fat) will contribute very little.

These oils contain modest amounts of vitamins and are sometimes used as replacements for cod liver oil for this reason. The properties and fatty acid compositions of these oils have not been reported, and it was hoped to find points of fatty acid composition differentiating commercial oils of comparable iodine values (I.V.).

The redfish (*Sebastes marinus* or *mentella*), also known as rosefish or ocean perch, is found, with exceptions, during the day in relatively deep water (100–300 fath) but at night feeds pelagically on euphausiids, etc. The characteristic pink tinge of this oil is probably due to euphausiids and thus to the distinctive feeding habits of the species (Crozier, 1967). Occasionally herring oils show similar but less intense hues. Much of the flatfish oil is sold as "flounder" oil since in Nova Scotia production is apt to be largely from the winter or blackback flounder (*Pseudopleuronectes americanus*). Other species of flatfish may be included in varying proportions. The blackback flounder is a shallow-water (<20 fath) species with a varied diet of bottom-living organisms. Further details of the distribution and biology of redfish and flounder are summarized by Leim and Scott (1966). The fishery for redfish is discussed by Templeman (1966).

Three random samples of commercial redfish oil and two different samples of flatfish oil were obtained from commercial sources in Nova Scotia. Analytical procedures followed those described by Ackman and Eaton (1966a) and the results are given in Tables I and II.

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TABLE I. Properties and fatty acid compositions of commercially produced redfish and flatfish oils.

Oil:	Redfish			Flatfish	
Year produced:	1960	1963	1965	1964(*a*)	1964(*b*)
Iodine value (Wijs):	115	119	125	141	150
Non-saponifiables, %:	1.85	1.08	1.30	1.14	1.03
Free fatty acid, %:	1.84	0.99	1.50	2.84	1.35
Fatty acid[a]	Fatty acid methyl ester composition, %				
			Saturated		
12:0	0.03	0.04	0.03	0.07	0.07
14:0[b]	4.19	4.87	2.49	4.97	6.12
15:0	0.34	0.35	0.30	0.51	0.51
Pristanic?	0.17	0.21	0.30	0.33	0.20
16:0	12.23	10.43	13.25	10.23	9.70
17:0[c]	0.34	0.43	0.61	0.25	0.50
18:0	2.21	2.88	2.16	3.01	2.94
19:0	Trace	0.06	Trace	0.13	0.39
20:0	0.38	0.35	0.20	0.08	0.43
Total	19.8	19.5	21.1	19.6	20.9
			Monounsaturated[d]		
14:1ω5[e]	0.77	0.49	0.35	0.92	0.53
16:1ω7	12.23	11.40	13.25	14.90	12.54
17:1ω8	0.22	0.22	0.42	0.30	0.42
18:1ω9	16.36	16.57	13.31	17.32	16.52
19:1ω8	0.17	Trace	0.10	0.15	0.11
20:1ω9	16.02	15.54	17.22	10.84	11.33
22:1ω11	18.69	17.00	18.90	9.64	9.02
24:1ω9	0.90	0.79	0.52	0.33	0.85
Total	65.5	62.0	63.9	54.4	51.3
			Diunsaturated		
16:2ω7 } [f] 16:2ω4 }	0.83	1.57	1.51	1.83	1.49
18:2ω6	1.23	0.55	0.94	0.84	0.94
20:2ω6	0.47	0.13	0.40	0.12	0.21
Total	2.5	2.3	2.9	2.8	2.6
			Triunsaturated		
16:3ω4	0.74	0.77	0.68	0.83	1.11
18:3ω6	Trace	Trace	0.14	Trace	0.03
18:3ω3	0.71	0.21	0.47	0.13	0.38
20:3ω6	0.18	0.05	0.18	Trace	Trace
22:3?	–	–	–	–	0.30
Total	1.6	1.0	1.5	1.0	1.5

(*Continued*)

TABLE I. Properties and fatty acid compositions of commercially produced redfish and flatfish oils. — (*Concluded*)

Oil:	Redfish			Flatfish	
Year produced:	1960	1963	1965	1964(*a*)	1964(*b*)
			Tetraunsaturated		
16:4ω1	0.89	0.40	1.40	0.50	0.54
18:4ω3	1.67	1.06	1.54	1.58	2.37
20:4ω6	0.45	0.30	0.30	1.05	0.73
20:4ω3	0.24	0.19	0.34	0.54	0.51
22:4ω6	Trace	0.02	Trace	Trace	Trace
Total	3.3	1.7	3.6	3.7	4.1
			Pentaunsaturated		
20:5ω3	6.20	8.01	7.31	11.12	12.27
21:5ω2 ?	0.29	0.26	0.27	0.46	0.67
22:5ω6	0.03	0.03	Trace	0.10	0.06
22:5ω3	0.36	0.57	0.47	1.33	1.37
Total	6.9	8.9	8.1	13.0	14.4
			Hexaunsaturated		
22:6ω3	2.58	4.25	3.33	4.83	4.57
I.V. calc. from GLC	114	117	120	139	146

[a]Shorthand notation for chain length:number of double bonds and position of ultimate double bond relative to terminal methyl group.
[b]Includes 4,8,12-trimethyltridecanoic acid.
[c]Includes phytanic acid.
[d]"ω" values refer to probable dominant isomer. Other isomers present in most instances.
[e]Includes *iso*- and *anteiso*-15:0.
[f]Includes *iso*- and *anteiso*-17:0.

The fatty acid compositions (Table I) are typical of triglyceride marine oils. There are usually wide fluctuations in percentages of particular fatty acids in various samples of the same marine oil but some possible general relationship may be discussed. An obvious difference in the two oils is the greater proportion of 20:1 and 22:1 in the redfish oil than in the flatfish oil. In particular the ratio 22:1 > 20:1 in the redfish oil is of interest as this is usually considered a characteristic of clupeid oils (Lambertsen and Braekkan, 1965; Ackman and Eaton, 1966a; Ackman et al., 1967). There is reason to associate this ratio of fatty acids (22:1 > 20:1) in fish oils with the dietary habits of clupeids and redfish and with the fatty acid composition of North Atlantic planktonic crustaceans such as *Meganyctiphanes norvegica* (Ackman and Eaton, 1966b; 1967). In the low I.V. oil from Greenland halibut (*Reinhardtius hippoglossoides*) 20:1 and 22:1 occur in about equal proportions (Ackman et al., 1967), but this deepwater species feeds at times heavily on capelin (*Mallotus villosus*). This may modify the depot fat in comparison

TABLE II. Composition in terms of major chain lengths and certain ratios of fatty acid types.

Oils:	Redfish			Flatfish	
Year produced:	1960	1963	1965	1964(*a*)	1964(*b*)
Chain length					
C_{14}	5.0	5.4	4.6	5.9	6.6
C_{16}	24.8	24.6	25.6	28.3	25.4
C_{18}	22.2	21.3	18.5	22.9	23.2
C_{20}	23.9	24.5	25.9	23.8	25.5
C_{22}	21.7	21.9	22.7	15.9	15.3
% polyunsaturates					
Experimental[a]	16.9	18.1	19.3	25.3	27.2
Calculated[b]	15.8	17.1	19.1	24.9	27.6
16:0 as % of saturated	61.5	53.4	62.8	52.2	46.4
16:1 + 18:1	28.6	28.0	26.6	32.2	29.1
16:0/(16:1 + 18:1)	0.43	0.37	0.50	0.32	0.34

[a]By GLC.
[b]From formula: % poly = 10.7 + 0.337 (oil I.V.–100).

with flatfish such as the flounder which feeds more definitely on smaller bottom fauna.

The proportions of 16:0 to total saturates for these oils (Table II) are not markedly different from the values (~60%) previously reported from this laboratory for oils of other species. The ratios for 16:0/(16:1 + 18.1) differentiate both redfish and flatfish oils from herring oils although not from Greenland halibut or sable fish(*Anoplopoma fimbria*) oil (Ackman and Eaton, 1966a; Ackman et al., 1967). In the polyunsaturated fatty acids there are no obviously unique features of either redfish or flatfish oil but the conversion 20:5ω3 → 22:6ω3, which gives nearly equal percentages of these two acids in cod (*Gadus morhua*) liver oil (Jangaard et al., 1967), evidently does not take place to the same extent in redfish and flatfish.

The fatty acid chain-length distributions (Table II) are informative. There is no emphasis on any one chain length in the redfish, whereas in clupeids and Greenland halibut a general rule $C_{16} > C_{18}$, and $C_{22} > C_{20}$ is noticeable in clupeid oils of I.V. less than 125 (Ackman and Eaton, 1966a; Ackman et al., 1967). The redfish oils, of which five samples collected from storage tanks in 1960, 1961, 1963, and 1965 had respective I.V. of 115, 115 and 116, 119, and 125, are thus distinguishable by chain-length distribution of fatty acids from other marine oils of comparable I.V. so far examined. It is not known if the apparent steady rise in I.V. over this period is associated with a shift in fishing pressures from large fish to small fish (Templeman, 1966), to increasing depth of fishing operations, or to other causes. Neither time of year of production nor locale of reduction (Louisbourg or Lunenburg) appeared to be associated

with I.V. variations. The flatfish oil is chiefly notable for the low proportion of C_{22} relative to C_{20}. This oil is broadly similar to cod liver oil (average I.V. 163) in composition. Average figures for cod liver oil chain-length composition are, for C_{16}, C_{18}, C_{20}, and C_{22}, respectively 23.7, 28.6, 21.4, and 19.8% (Jangaard et al., 1967). The difference in the flatfish percentages for C_{18}, lower than C_{16} or C_{20}, is thus a definite dissimilarity when compared with cod liver oil. It thus appears possible that at least some commercial oils of comparable I.V. can be distinguished by differences in proportions of certain fatty acids and of fatty acid chain lengths.

Fisheries Research Board of Canada
Halifax Laboratory, Halifax, N.S.

R. G. ACKMAN
P. J. KE

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REFERENCES

ACKMAN, R. G., AND C. A. EATON. 1966a. Some commercial Atlantic herring oils: fatty acid composition. J. Fish. Res .Bd. Canada, **23**(7): 991–1006.

1966b. Lipids of the fin whale (*Balaenoptera physalus*) from North Atlantic waters. III. Occurrence of eicosenoic and docosenoic fatty acids in the zooplankter *Meganyctiphanes norvegica* (M. Sars) and their effect on whale oil composition. Canadian J. Biochem., **44**: 1561–1566.

1967. Fatty acid composition of the decapod shrimp, *Pandalus borealis*, in relation to that of the euphausid, *Meganyctiphanes norvegica*. J. Fish. Res. Bd. Canada, **24**(2): 467–471.

ACKMAN, R. G., C. A. EATON, AND P. J. KE. 1967. Canadian marine oils of low iodine value: Fatty acid composition of oils from Newfoundland turbot (Greenland halibut), certain Atlantic herring, and a sablefish. J. Fish. Res .Bd. Canada, **24**(12): 2563–2572.

BAILEY, B. E. 1952. Marine oils with particular reference to those of Canada. Bull. Fish. Res. Bd. Canada, No. 89. 413 p.

CROZIER, G. F. 1967. Carotenoids of seven species of *Sebastodes*. Comp. Biochem. Physiol., **23**: 179–184.

JANGAARD, P. M., R. G. ACKMAN, AND J. C. SIPOS. 1967. Seasonal changes in fatty acid composition of cod liver, flesh, roe and milt lipids. J. Fish. Res. Bd. Canada, **24**(3): 613–627.

LAMBERTSEN, G., AND O. R. BRAEKKAN. 1965. The fatty acid composition of herring oils. Fiskeridirektorat. Skrifter Ser. Teknol. Undersock., **4**(13): 15 p.

LEIM, A. H., AND W. B. SCOTT. 1966. Fishes of the Atlantic Coast of Canada. Bull. Fish. Res. Bd. Canada, No. 155. 485 p.

TEMPLEMAN, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Bd. Canada, No. 154. 170 p.

Comparison of the Otolith and Scale Methods for Aging Sockeye (*Oncorhynchus nerka*) and Chum (*O. keta*) Salmon

As Pacific salmon approach the final spawning act, their scales become absorbed so that only the centers remain in the scale pockets. Consequently, the total age of such a fish cannot be estimated from the scale markings because the portions which were last formed no longer exist. Another method of estimating the age of fish is by examination of their otoliths. Clutter and Whitesel (1956) suggested that otoliths from spawning Fraser River sockeye were useful for estimating the number of winters at sea but that the number of winters spent in fresh water could be estimated more easily from examination of the remnants of the scales.

The purpose of this note is to compare estimates of freshwater and ocean ages as estimated from scales and otoliths obtained from sockeye and chum salmon before the onset of scale absorption.

Materials and methods.— In 1964 scales and otoliths were removed from sockeye and chum salmon (as detailed in Table I) and preserved. In the laboratory plastic impressions were made of the scales and the otoliths were placed in pure glycerin. Otoliths were examined under a binocular microscope over a black background using reflected light. The otolith, which is composed of alternating layers of translucent and opaque material, appears in flat aspect to consist of alternating light and dark bands (Fig. 1 and 2). The translucent band, which appears dark, is taken to represent material deposited during the winter and is called an annual ring. It is comparable with the winter bands or annuli on the scales. The scales were examined as projected images at 100 magnifications.

Aging of each fish by otoliths and scales was done at different times. In some cases the fish were first aged from their scales and in others the ages were first determined from either scales or otoliths. In no instance were ages, previously determined from either scales or otoliths, referred to when samples were aged by the alternative method.

Results.— Estimates of age made by using scales and otoliths are compared in Table I. It is apparent that the two methods generally lead to the same age estimates, the poorest agreement being 88.6% for the samples of Rivers Inlet sockeye. Paired estimates are presented in Table II for cases in which the estimates of age differed. Of the Skeena area sockeye five of eight disagreements were on the estimation of freshwater age. For the Rivers Inlet sockeye 9 of 10 disagreements were on the estimation of freshwater age. In contrast all three of the Fraser sockeye disagreements were in the estimation of ocean annuli. These data may indicate problems associated with particular stocks. In general the disagreements tended to be associated with misclassification of environment rather than with recognition of annuli. Among the 21 sockeye where age estimates disagreed there was only one case where the

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TABLE I. Samples of sockeye and chum salmon used for comparison of age estimates made using scales and otoliths.

	Total no. sampled	Readable	Age agreed	
			No.	%
	Sockeye			
Skeena River estuary	199	181	177	97.8
Skeena River area	199	170	166	97.6
Rivers Inlet area	100	88	78	88.6
Fraser River area	49	39	36	92.3
	Chum			
Bella Coola area	294	265	251	94.7
Fraser River area	50	46	42	91.3

TABLE II. Comparison of ages[a] of sockeye and chum salmon as determined from scales and otoliths which were in disagreement.

Species	Areas	No.	Scales	Otoliths
Sockeye	Skeena River estuary	1	1.3	1.2
		1	1.3	2.3
		1	0.3	1.2
		1	1.2	2.2
	Skeena River area	1	1.2	2.2
		1	1.2	1.3
		1	1.3	1.2
		1	2.2	1.2
	Rivers Inlet area	1	2.2	1.3
		1	1.2	2.2
		4	1.3	2.3
		1	1.2	1.3
		2	2.3	1.3
		1	0.3	1.3
	Fraser River area	3	1.3	1.2
Chum	Bella Coola area	5	0.3	0.2
		3	0.3	0.4
		3	0.4	0.3
		3	0.2	0.3
	Fraser River area	2	0.2	0.3
		1	0.3	0.2
		1	0.3	0.4

[a]The European system of age designation (Koo, 1962) is used in this report.

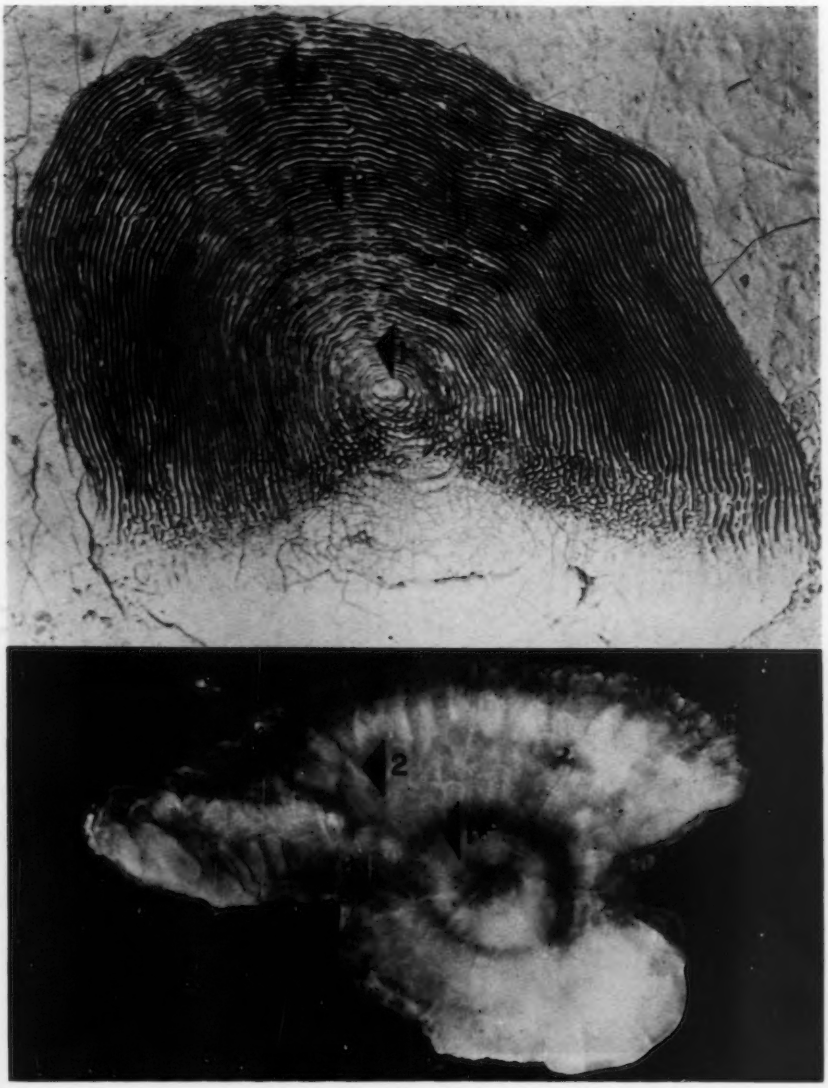

FIG. 1. A scale and otolith from a 1.2 sockeye salmon.

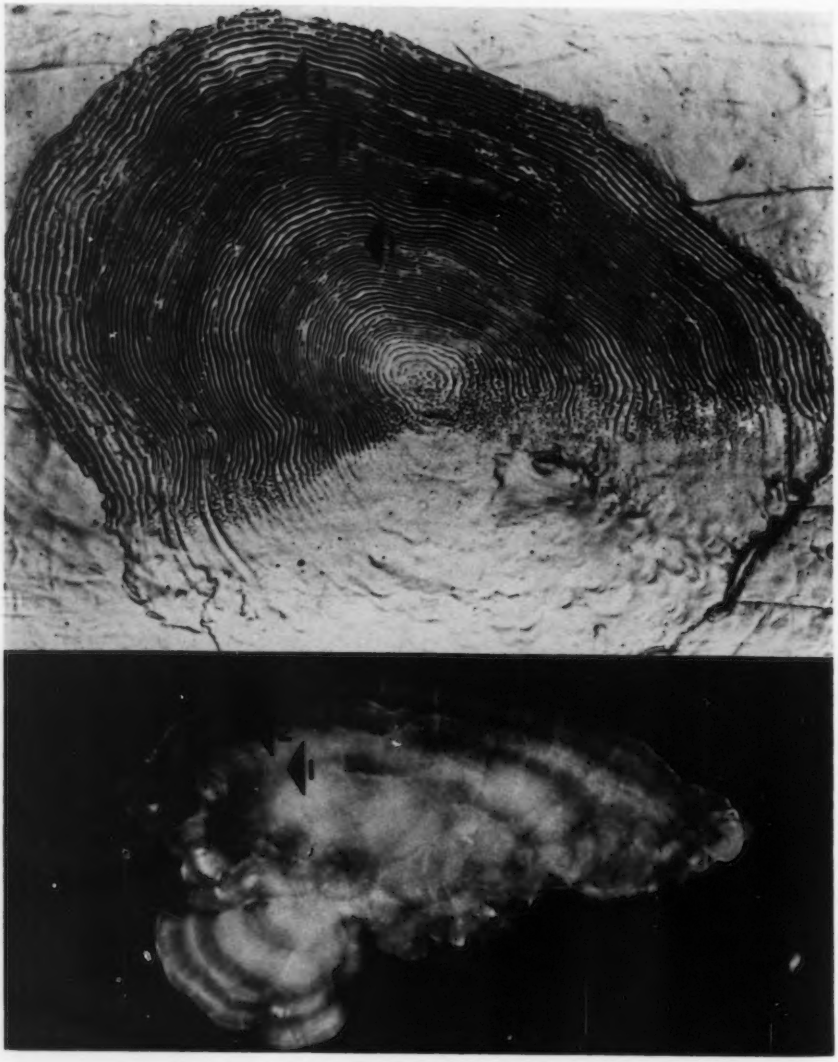

FIG. 2. A scale and otolith from a 0.3 chum salmon.

total age estimates agreed. In 9 cases older total ages and in 11 cases younger total ages were estimated by using scales rather than using otoliths. Among the 18 chums, older ages were estimated in 9 cases and younger ages estimated in 9 cases by using scales rather than by using otoliths. It is concluded from these data that there is no relative bias in either method of aging; both methods should yield similar results in large samples.

Most collections of salmon scales contain some scales that are regenerated. These are unusable because much or most of the early life history of the fish is missing. As a result there are always some scale samples which have to be discarded. For sockeye the proportion of regenerated scales among the samples varied from 8 to 20% and for chums from 4 to 6%. The proportion of otoliths that was unreadable (because they were either broken or appeared cloudy) for sockeye varied from 0 to 0.5% and for chums from 3 to 4%. Thus the portion of unreadable otoliths in the samples of sockeye, but not chum salmon, was considerably smaller than the portion of unreadable scales.

Aging of salmon from otoliths is considerably more time consuming, taking longer to collect and to read, and involves the death of the fish. Therefore, where large volumes of samples are involved and/or the fish is to be released alive, only the scale method is possible. On the other hand, where small numbers of fish are involved or the scales are incomplete either from absorption or regeneration, the otolith method will provide a similar age classification.

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Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

H. T. Bilton
D. W. Jenkinson

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REFERENCES

Clutter, R. I., and L. E. Whitesel. 1956. Collection and interpretation of sockeye salmon scales. Intern. Pacific Salmon. Comm. Bull. IX. p. 1–159.

Koo, Ted S. Y. 1962. Age designation in salmon. Studies of Alaska red salmon. University of Washington Press, Seattle, Wash. p. 37–48.

Occurrence of the Larvae of *Meganyctiphanes norvegica* (Crustacea, Euphausiacea) off West Greenland

From April to August 1963, the plankton of the Northwest Atlantic was surveyed during a programme organized by the International Commission for the Northwest Atlantic Fisheries. This survey, designated NORWESTLANT, entailed the co-operation of several countries, and the Hensen-net samples collected by the Danish research ship *Dana* west of Greenland were analysed in Edinburgh. *Dana* made two cruises, the first from May 25–June 14 and the second from June 30–July 16. In Fig. 1 is shown the combined survey area of the two cruises; it has been divided into rectangles of 1° long by 30′ lat.

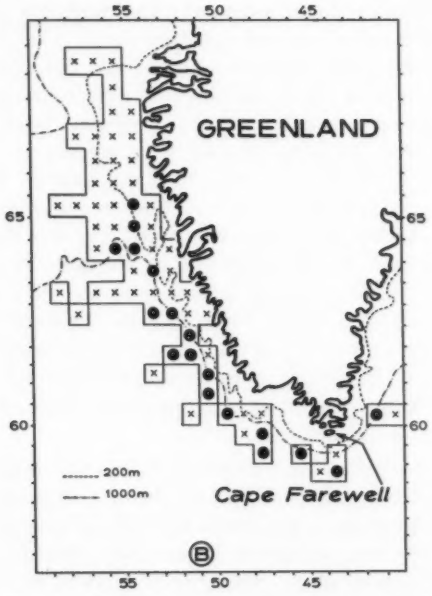

FIG. 1. The occurrence of calyptopes and furcilias of *Meganyctiphanes norvegica* off the west coast of Greenland. Their presence is indicated by solid circles and absence by crosses. The area sampled by R. V. *Dana* is outlined. The encircled letter B indicates the position of Weather Ship Station *Bravo*.

Meganyctiphanes norvegica (M. Sars) is an important member of the zooplankton over the continental slope and shelf waters of the northern Atlantic and Mediterranean (Einarsson, 1945). Although adults of this species

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are known from waters off West Greenland, evidently they are not very abundant (Kramp, 1963; Nosova, 1966) and in the view of Einarsson, "a limited number of individuals may be brought with the currents but most probably these never mature, although they may live for several years and reach great size." This opinion has been reiterated recently by Mauchline and Fisher (1967). The occurrence of the larvae of *M. norvegica* in the eastern Labrador Sea is thus of some interest.

The samples from the first cruise of *Dana* contained only the first and second calyptopis stages. In the second cruise the first two furcilias predominated, although some second and third calyptopis stages and later furcilia stages were present. The estimated density of the furcilias never exceeded 2 per 10 m^3. This may be compared with estimates of up to 150 per 10 m^3 for furcilias of *Thysanoessa longicaudata* (Krøyer) and 90 per 10 m^3 for furcilias of *T. inermis* (Krøyer) from the same series of samples.

The occurrence of the larval stages of *M. norvegica* in the eastern Labrador Sea is not proof that spawning had occurred there. The area is in the path of the northerly flowing West Greenland Current, the greater part of which flows along the Greenland Shelf. However, it also influences the slope waters, in which the larvae were found. Cape Farewell may be taken as the western limit of the recognized breeding area of *M. norvegica*, from which the larvae could have drifted. During the NORWESTLANT cruises the rate of flow of the slope waters was 5–6 miles per day and the temperature of the upper 100 m was 4–5 C (Campbell et al., MS, 1964). At this temperature the time between spawning and the development of the second calyptopis is about 20 days (Heegaard, 1948), during which time the larvae could have been carried approximately 120 miles. The distances between Cape Farewell and the most northerly occurrences of the second calyptopis stages on the first and second cruises of the *Dana* were about 250 and 400 miles respectively. It is probable, therefore, that breeding does take place, if only infrequently, in the waters west of Greenland.

The nearest reported location of larval *M. norvegica* is at Weather Station *Bravo* (Fig. 1), where Kielhorn (1952) found a first stage calyptopis at the end of May. The temperature there was about 5 C; this information, together with that presented here, supports Einarsson's (1945) suggestion that the northern limit of breeding of *M. norvegica* is marked by the 5 C surface isotherm in May.

I am grateful to the Director of Danmarks Fiskeri-og Havundersøgelser who made the plankton collections available for analysis in Edinburgh.

Scottish Marine Biological Association
Oceanographic Laboratory, Edinburgh, Scotland

LESLIE T. JONES

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REFERENCES

CAMPBELL, N. J., J. R. N. LAZIER, AND R. H. LOUCKS. MS, 1964. Preliminary assessment of the physical oceanography of the Labrador Sea during NORWESTLANT-2, 1963. Unpublished MS, Bedford Inst. Oceanog., Dartmouth, N.S. 33 p.

EINARSSON, H. 1945. Euphausiacea. I. Northern Atlantic species. Dana Rept., 5(27): 1–185.

HEEGAARD, P. 1948. Larval stages of *Meganyctiphanes* (Euphausiacea) and some general phylogenetic remarks. Medd. Komm. Danmarks Fiskeri-og Havendersøgelser Ser. Plankton, 5(1): 1–27.

KIELHORN, W. V. 1952. The biology of the surface zone zooplankton of a boreo-arctic Atlantic Ocean area. J. Fish. Res. Bd. Canada, 9: 223–264.

KRAMP, P. L. 1963. Summary of the zoological results of the "Godthaab" Expedition 1928. Medd. Grønland, 81(7): 1–115.

MAUCHLINE, J., AND L. R. FISHER. 1967. Distribution of the euphausiid crustacean *Meganyctiphanes norvegica* (M. Sars). Ser. Atlas Marine Environ., Folio 13. 3 p., 3 pl.

NOSOVA, E. K. 1966. [The species composition and quantitative distribution of euphausiids off West Greenland. Data on Fisheries Research in the Northern Basin.] Pt. 7. p. 125–128. PINRO. (In Russian.)

An Occurrence of the Pelagic Stingray *Dasyatis violacea* in the Northwest Atlantic

A pelagic stingray *Dasyatis violacea* (Bonaparte) 1882 taken near the eastern edge of the Grand Bank (46°19'N lat, 44°43'W long) on September 6, 1967, was caught on a surface line trawl from the Fisheries Research Board's research vessel *A. T. Cameron*. It was hooked through the posterior portion of the left pectoral fin. The specimen is stored in the Royal Ontario Museum (cat. no. 25,636).

The occurrence of *D. violacea* in the Northwest Atlantic was recorded by Bigelow and Schroeder (1962, 1965). They reported details of capture and morphometrics for four female specimens — three from the area between Georges Bank and Chesapeake Bay, and the fourth far offshore at 34°40'N lat, 44°50'W long. Our specimen was also a female, and apparently immature. It was captured nearly 700 miles farther north than any of the four reported by Bigelow and Schroeder.

Body measurements in millimeters and as percentages of the disc width are given in Table I. This method of reporting is in conformity with that of Bigelow and Schroeder (1962).

TABLE I. Morphometric data for one female specimen of *Dasyatis violacea*. Body measurement expressed as percentage of disc width in parentheses.

	mm
Total length	741.0
Snout to anterior border of cloaca	289.0 (62.9)
Tail length (anterior border of cloaca to tip)	452.0 (98.5)
Anterior cloaca to origin of tail spine	152.0 (33.1)
Disc: length	350.0 (76.3)
width	459.0
Snout: before orbit	61.0 (13.3)
before mouth	65.5 (14.3)
Nostrils: distance between inners	41.0 (8.9)
Eye: exposed horizontal diam	13.0 (2.8)
interorbital distance	71.0 (15.5)
Spiracle: horizontal length	32.5 (5.1)
interspiracular distance	70.0 (15.3)
Spine length	101.0 (22.0)
Mouth width	48.0 (10.5)
Gills: opening length (right & left); 1st	12.5 (2.7) + 12.0 (2.6)
3rd	13.0 (2.8) + 14.0 (3.0)
5th	6.5 (1.4) + 6.5 (1.4)
distance between inners; 1st	82.5 (18.0)
5th	57.0 (12.4)
Cloacal opening length	25.0 (5.4)

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In addition to extending the known range and adding to our knowledge of the morphometry of this species, which is apparently rare in the Northwest Atlantic, the present capture provided new information on colour. The specimen was alive when boated and it was noted that the intensely black dorsal and ventral surfaces (Fig. 1) were both covered with a thick but delicate black mucus. However, even with careful handling, large quantities of the black mucus adhered to both rubber gloves and to the backdrop sheet used for photography. The ash-gray and light-brown colours previously recorded (Bigelow and Schroeder, 1965) may have resulted from a combination of handling and preservation. Our specimen is now grayish, in distinct contrast to the vivid black of the living fish.

Royal Ontario Museum
Toronto, Ontario
W. B. SCOTT

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.
S. N. TIBBO

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REFERENCES

BIGELOW, H. B., AND W. C. SCHROEDER. 1962. New and little known batoid fishes from the western Atlantic. Bull. Museum Comp. Zool., Harvard Univ., **128**(4): 159–244.

1965. A further account of batoid fishes from the western Atlantic. Ibid., **132**(5): 443–477.

(FIG. 1 *opposite*)

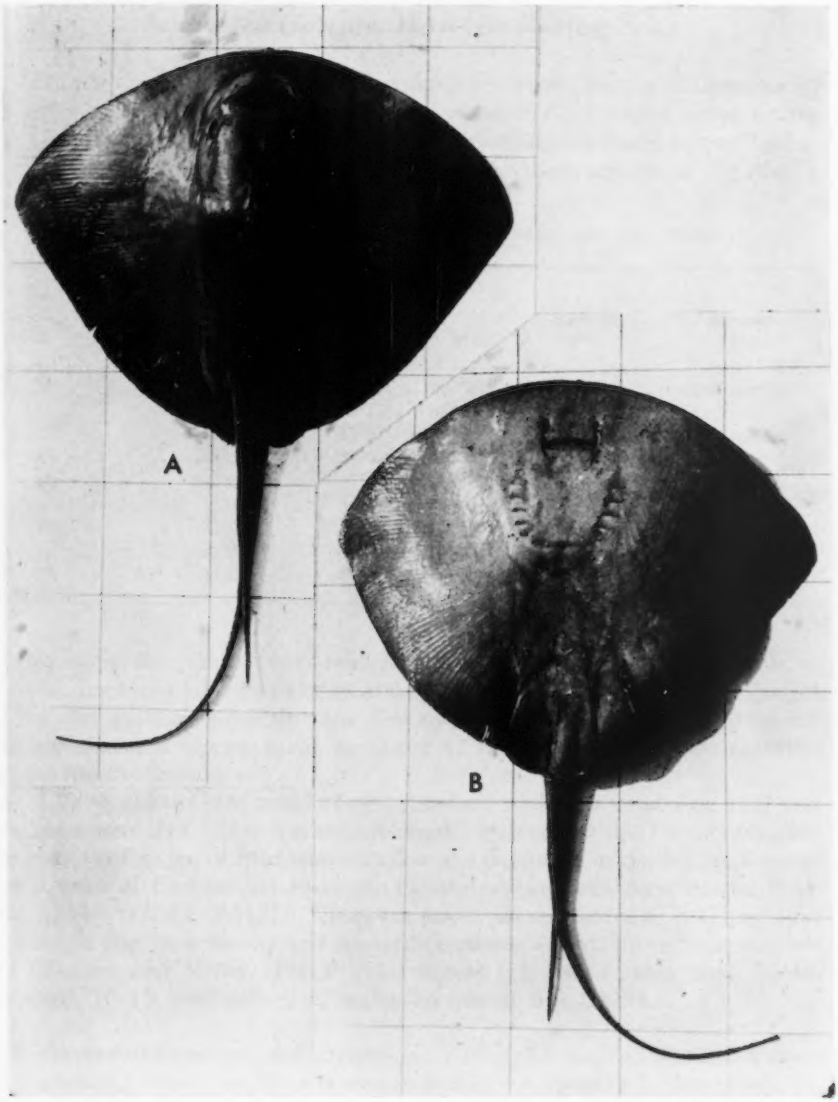

FIG. 1. (A) Dorsal view and (B) ventral view of *Dasyatis violacea*, female, 741 mm total length.

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Extension of Recorded Range of Butter Sole, *Isopsetta isolepis*, Into the Bering Sea

During the 1964 summer shrimp exploratory cruise, Bureau of Commercial Fisheries personnel aboard the chartered vessel M/V *Paragon* noted butter sole, *Isopsetta isolepis* (Lockington) 1880, in trawl catches made at nine fishing stations (Table I) in the Bering Sea, near the northwestern tip of the Alaska

TABLE I. Stations in the Bering Sea where butter sole were taken.

Date (1964)	Station No.	Position		Depth (*m*)	Bottom type
		N lat	W long		
Aug. 24	1122	55°08′	164°30′	75–79	Sand, gravel
	1126	55°28′	163°29′	68–71	Sand
	1127	55°27′	163°19′	55–60	Sand, gravel
" 25	1128	55°32′	163°02′	51–51	Sand
" 26	1130	55°54′	162°29′	71–71	"
	1131	56°01′	162°14′	73–75	"
" 27	1132	56°10′	162°02′	68–71	"
	1133	56°06′	161°35′	46–49	"
" 29	1135	56°23′	161°31′	66–69	"

Peninsula. Wilimovsky (1964) reported the western range of butter sole to include Amchitka Island in the central Aleutian chain. The butter sole caught at the nine stations constitute the first records in the Bering Sea and extend the northwestern known range to about 42 miles northwest of Port Moller on the Alaska Peninsula.

Two specimens (167 and 197 mm standard length) from station 1122 and five specimens (143–167 mm standard length) from station 1127 were preserved for later verification of field identification and deposited in the fish museum of the Bureau of Commercial Fisheries Laboratory at Auke Bay, Alaska (Cat. No. AB66-1122, AB66-1127). The seven preserved specimens fit the diagnostic characters and their fin-ray and lateral-line counts are within the ranges given by Clemens and Wilby (1961). Fins: dorsal (1), 84–89 rays; anal, 63–69; pectoral, 10–13; and pelvic, 6. Scales on lateral line, 78–84.

U.S. Bureau of Commercial Fisheries
Exploratory Fishing and Gear Research Base
Juneau, Alaska

MITSUO YESAKI
ROBERT J. WOLOTIRA, JR.

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REFERENCES

CLEMENS, W. A., AND G. V. WILBY. 1961. Fishes of the Pacific Coast of Canada. Bull. Fish. Res. Bd. Canada, No. 68 (2nd ed.). 443 p.

WILIMOVSKY, N. J. 1964. Inshore fish fauna of the Aleutian Archipelago. Science in Alaska. Proc. Fourteenth Alaskan Sci. Conf. Aug. 27–30, 1963. p. 172–190.

Observation of Inertial Oscillation in the Northwest Atlantic at 42°N

Ocean currents have been measured throughout the world for many years using meters suspended from anchored ships. Defant (1961) has summarized many observations of inertial oscillations. However, in the deep ocean, it is difficult to assess the effect of a ship's movement on the data (Bowden, 1954). Recent advances in instrumentation (e.g., GEK and self-recording current meters) have made it possible to avoid the anchored-ship technique. Reid (1962) has concluded from his own GEK measurements at 30°N and from a careful examination of earlier anchored-ship observations that, in the deep ocean, strong inertial oscillations may occur near 30° lat where there is resonance with the diurnal tidal forces, but that at other latitudes they are either weak or nonexistent. More recent measurements, however, have shown that inertial oscillations can be strong at other latitudes as well (47°N (Rattray, 1962); 33°N–41°N (Webster, 1963); and 42°N (present discussion)).

In 1964, two cruises were carried out by the Bedford Institute of Oceanography in order to develop techniques for mooring current meters in the deep ocean. Moorings were laid at several sites along a line starting at the edge of the Continental Shelf near Sable Island and running southeast (insert, Fig. 1). Due to the experimental nature of the project, only a limited amount of current data were obtained. The purpose of this report is to describe in some detail the inertial current observed at station 3.

Equipment.— Station 3 was located at 42°12′N; 56°42′W at a depth of 4630 m (insert, Fig. 1). The first mooring was laid on September 17 and used a 10-mm diam stranded polypropylene line with an unstretched length equal to 93% of the depth, and was supported by a surface buoy. Current meters were attached at depths of 180, 1370, and 2750 m. They were Braincon type 316 Histogram meters that use a Savonius rotor to measure speed and a large tail fin to align the instrument case with the current. The direction is detected by a magnetic compass. During a 19-min recording interval, an arc proportional to total rotor movement and a histogram of the tail fin direction are both recorded on 16-mm film. The last minute of each cycle is used to advance the film. Thus over a recording cycle, one has a measure of the average speed and the most frequent direction. Tilt magnitude and direction are also recorded and used to make corrections to the rotor readings. They can also give some idea of the configuration of the mooring.

The first mooring was recovered after 4 days. It was found that the lower parts of the tail fins on all three instruments were missing, possibly due to too rapid lowering. The loss of fin area by itself would not have been serious, but the missing portions held counterweights designed to balance the instruments about the axis of suspension. Without the counterweights the unbalanced

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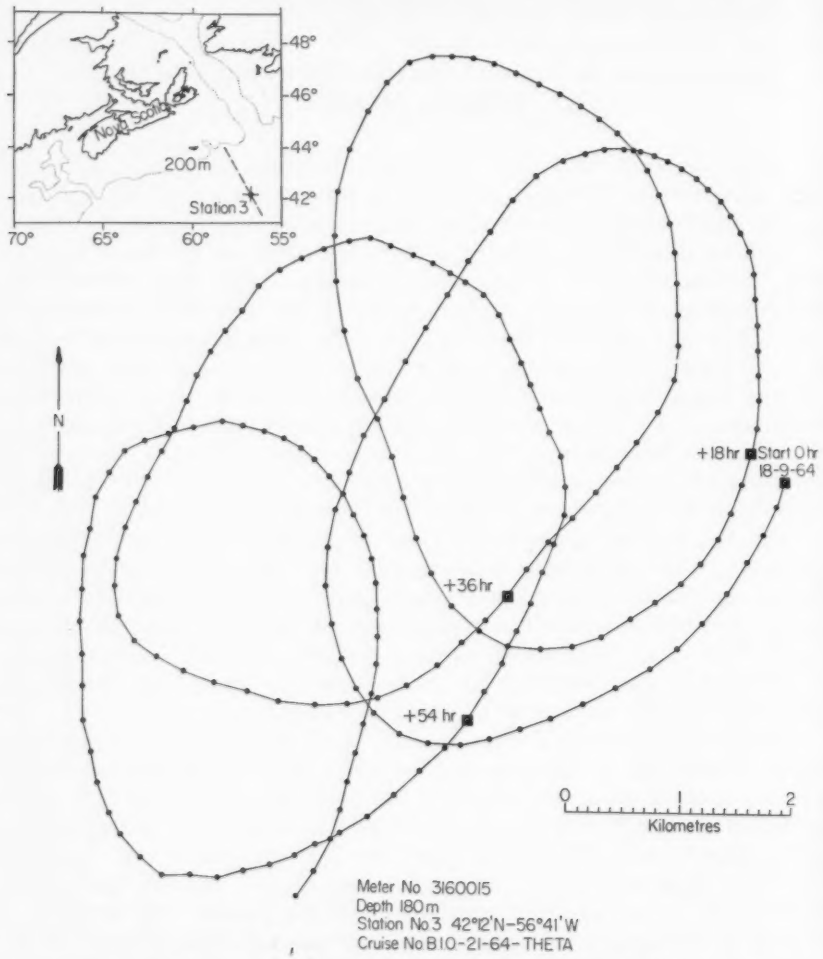

FIG. 1. Progressive vector diagram of the current at 180 m depth at station 3 (42°12′N; 56°41′W) as measured by a Braincon type 316 Histogram Current Meter. The data points are 20 min apart in time and the square symbols mark every 54th point (18 hr). The theoretical inertial period at this latitude is 17.8 hr. The insert map shows the location of the station on a section line extending out from the Continental Shelf off Nova Scotia.

instrument cases tended to lie on the low side of the mooring line so that the current direction was not properly recorded. However, for the uppermost current meter (180 m depth), the measured tilt direction can be used in place of the current direction if it is assumed that the current direction is approximately constant with depth from the surface to 180 m (for any mooring, the tilt direction at a given depth is the direction of the vector sum of the drag

forces on the entire portion of the mooring above that depth). This assumption was not considered valid at greater depths, so the data from the lower two current meters were not used.

The second mooring was laid on October 2 and used a 16-mm diam stranded polypropylene line with an unstretched length equal to 95% of the depth. The current meters were Geodyne type A-100 that use a Savonius rotor to measure speed and a small vane that moves independently of the case to measure direction. The rate and direction are sampled for 1 min out of every 5 and recorded in digital format on 16-mm film. The film failed to advance in the lowest meter, but the upper two (180 and 1370 m) functioned satisfactorily.

Results.— The data from the first mooring at station 3 (Fig. 1) show there was a strong clockwise rotary current. The progressive vector plot is the path that a water particle would follow if the current were uniform over an area at least as large as that covered by the diagram. The displacement of the loops indicates that there was a small residual current whose direction changed appreciably partway through the record.

The currents were also resolved along north and east directions to create two time series. The value of the inertial period at the latitude of station 3 is 17.80 hr. A curve having this period was fitted separately to these two time series using the method of least squares. The amplitudes obtained for the north and east series respectively were 23.0 and 18.5 cm/sec. The amplitude ratio was 1.24:1 and the phase difference 77°, whereas for a purely rotary motion the values would be 1.00 and 90°. The phases of the two series referred to 0 hr September 18, 1964 were 154° and 231°.

The data from the second mooring at station 3 had to be taken from the analog chart records produced by the automatic film reading machine rather than from its digital magnetic tape output, and this reduced the accuracy somewhat. In addition there was considerable noise in the direction channel, a fault common to the early Geodyne meters. The points were picked off at time intervals convenient for the initial harmonic analyses, which were done by hand. The clockwise inertial movement was evident at 180 m (Fig. 2),

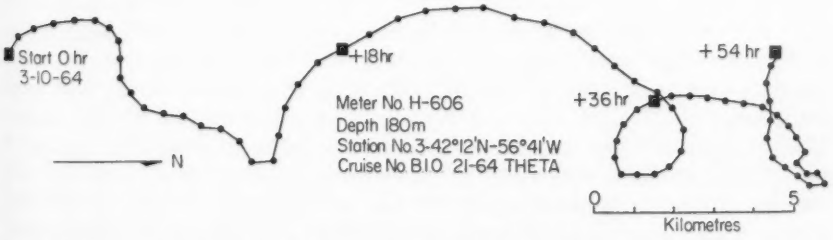

FIG. 2. Progressive vector diagram of the current at 180 m depth at station 3 (42°12′N; 56°41′W) as measured by a Geodyne type A-100 current meter. The data points were taken from an analog chart record at 44.7-min intervals, and square symbols mark every 24th point (17.9 hr). The theoretical inertial period at this latitude is 17.8 hr.

although the loops were irregular and somewhat spread out by the presence of a steady northward current. The least squares curve fitting at the inertial period gave amplitudes of 10.6 and 14.9 cm/sec for the north and east series, with an amplitude ratio of 1.41:1 and a phase difference of 81°. The phases of the two time series referred to 0 hr September 18, 1964 were 163° and 244°. At 1370 m (Fig. 3), the analyses gave amplitudes that were below 4 cm/sec and a phase difference of only 37°.

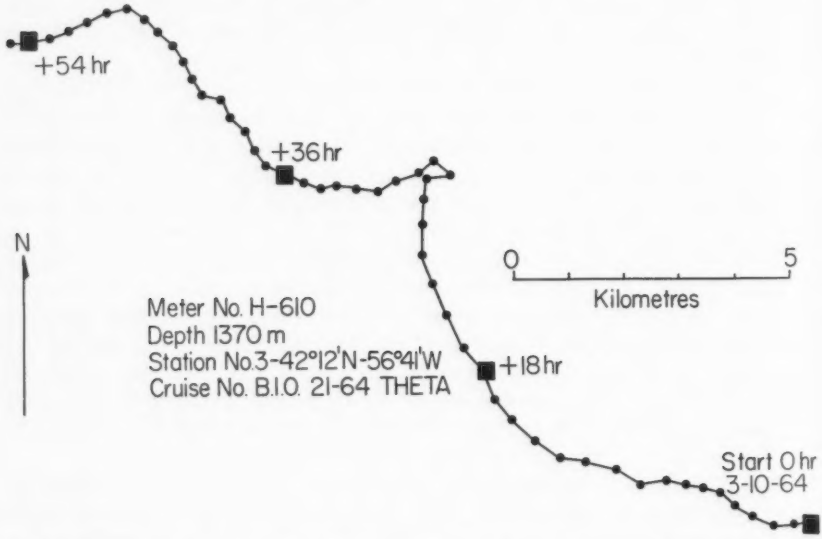

FIG. 3. Progressive vector diagram of the current at 1370 m depth at station 3 (42°12'N; 56°41'W) as measured by a Geodyne type A-100 current meter. The data points were taken from an analog chart record at 62-min intervals and square symbols mark every 17th point (17.6 hr). The theoretical inertial period at this latitude is 17.8 hr.

Discussion.— The data from the first mooring at station 3 (Fig. 1) clearly show a strong inertial oscillation at 180 m depth. Data taken 15 days later (Fig. 2, 3) show that the inertial oscillation was again present, although somewhat weaker and more irregular. The phase shifts for the north and east components were very small, 9° and 13°, indicating that the oscillation had been continuous for 17 days. Day and Webster (1965) analyzed an 85-day record from a much different location and found inertial oscillations that persisted for 10–15 days. There are no data to enable the horizontal extent of this present inertial current to be determined, but the current meter at 1370 m showed that it had no significant amplitude at that depth. The only other information about the upper layers obtained from these two cruises was 2 months earlier at station 2, 125 km to the northwest. At 140 m depth there was no significant inertial oscillation present over a 5-day period.

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Dept. of Energy, Mines and Resources
Bedford Institute, Dartmouth, N.S.

D. J. LAWRENCE

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REFERENCES

BOWDEN, K. F. 1954. The direct measurement of subsurface currents in the oceans. Deep-Sea Res., **2**(1): 33–47.

DAY, C. G., AND F. WEBSTER. 1965. Some current measurements in the Sargasso Sea. Ibid., **12**(6): 805–814.

DEFANT, A. 1961. Physical oceanography, Vol. 1. Chapter XIII, Section 6(C). Pergamon Press, London.

RATTRAY, M., JR. 1962. GEK observations of inertial oscillations. J. Geophys. Res., **67** (2): 1654, abstr. only.

REID, J. L., JR. 1962. Observations of inertial rotation and internal waves. Deep-Sea Res., **9**(4): 283–290.

WEBSTER, F. 1963. A preliminary analysis of some Richardson current meter records. Ibid., **10**(3): 389–396.

Food of Pacific Salmon and Steelhead Trout in the Northeast Pacific Ocean

Although Pacific salmon (genus *Oncorhynchus*) and steelhead trout (*Salmo gairdneri*) in the northeast Pacific Ocean have been the subject of considerable study over the past decade, published information on their food would appear to be limited to the spring and summer seasons. This article reports on observations on the food of salmonids, mainly sockeye (*O. nerka*) and pinks (*O. gorbuscha*) caught north of 45°N and east of 155°W during the winter (January 7–February 8, 1964) and compares these with those obtained during spring and early summer (May and June, 1958) reported by LeBrasseur (1966).

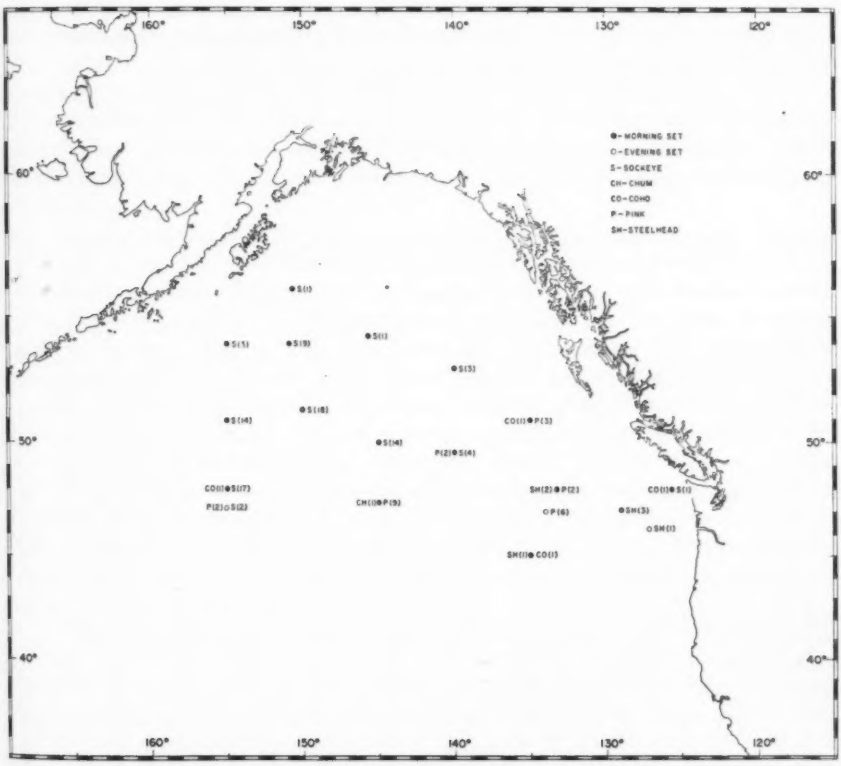

FIG. 1. Places of capture and numbers of salmon and steelhead trout examined for feeding habits, northeast Pacific Ocean, January 7–February 8, 1964.

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Figure 1 indicates the places of capture and the numbers of fish of each species examined. The fish were caught from the Fisheries Research Board vessel *G. B. Reed* using surface longlines. Most of the catches were made at dawn, but some were also made during approaching dusk. Upon completion of each haul, data were obtained on size, sex, and age from fish selected at random from the catch.

Organisms consumed.— Stomach contents were analysed at sea in the ship's laboratory. For each fish the total volume of contents was measured by water displacement in a graduated cylinder. The contents were then placed in a Petri dish and identified according to taxonomic categories, mainly family, with the aid of a binocular microscope. Volumes of individual categories were then determined either by direct measurement or by converting visual estimates of its percentage contribution to the stomach contents into volumetric terms. The relative importance of each category in the diet of a particular species of salmon was determined from its frequency of occurrence and its percentage contribution to the combined volume of contents. Parasites and baits were excluded from the contents. Data on numbers and sizes of salmon examined and their food are summarized in Table I.

The sockeye examined, which according to subsequent scale analyses had been at sea from a few months up to almost 3 years, fed predominately on fish (*Lampanyctus leucopsarus* and *Tarletonbeania crenularis*) of the family Myctophidae. Squid (other than bait) ranked second in importance. Other

TABLE I. Relative importance of various organisms in the winter diet of Pacific salmon and steelhead trout in the northeast Pacific Ocean, January 7 to February 8, 1964.

Species:	Sockeye		Pink		Coho		Steelhead	
No. examined:	87		24		4		7	
Length (fork) range (*cm*):	26.5–59.0		26.0–36.5		34.0–40.5		44.0–74.0	
No. with food:	44		15		2		4	
Total volume of contents (*cc*):	202.3		52.4		0.5		18.0	
Organism	F[a]	V[b]	F	V	F	V	F	V
Amphipod	11	<1	42	97	50	5	0	0
Pteropod	2	<1	0	0	25	<1	0	0
Euphausiid	5	<1	13	1	25	15	14	<1
Decapod	3	1	0	0	25	80	0	0
Isopod	2	<1	0	0	0	0	0	0
Ostracod	0	0	0	<1	0	0	0	0
Octopod	0	0	0	0	0	0	14	60
Squid	16	27	8	<1	0	0	43	21
Fish	35	71	13	1	0	0	14	10
Unidentifiable	2	<1	13	<1	0	0	14	9

[a]F = percentage of total fish examined containing food organism in stomach.
[b]V = percentage which particular food organism made of total volume of combined stomach contents.

organisms included amphipods, pteropods, euphausiids, and isopods but none of these groups was important.

Of 87 sockeye stomachs examined, 43 were devoid of food. Undiscernible from the data in Table I is the fact that at fishing sites where nine or more sockeye were examined, the percentage of fish with empty stomachs ranged from 22 to 94%. The highest incidence of fish with empty stomachs (16 of 17) occurred at 48°N, 155°W. These fish, on the average, were smaller (in weight and fork length) than those taken elsewhere. From age, size, and tagging data presented elsewhere (Anon., 1966), a large fraction, if not all, of the fish in this locality were probably in their penultimate year. Although LeBrasseur (1966) noted significant differences in feeding of immature and maturing sockeye during spring and summer, no explanation of the relatively few feeding fish during winter in this locality can be offered.

Pink salmon, which were in their final year of life, were feeding almost exclusively on hyperiid amphipods. This item was present in 10 of 15 fish having food in their stomachs. Other organisms encountered included euphausiids, ostracods, fish and squid.

Of four cohoes (*O. kisutch*) examined, two had food in their stomachs. Decapod crustaceans were the most important items found.

Four of the seven steelheads examined contained food in their stomachs. Judging from occurrence, the most important organisms were squid.

The stomach contents of the single chum (*O. keta*) (42.5 cm) were digested beyond recognition.

Seasonal differences in feeding habits.— Seasonal differences in the food of sockeye and pink salmon in the northeast Pacific Ocean were determined by comparing data collected during January with those of LeBrasseur (1965) for May and June, 1958. LeBrasseur's data are from catches made by surface gillnets during hours of darkness. From the proportions of fish with food in their stomachs LeBrasseur (1966) postulated that sockeye and pinks fed most actively in the early morning. Results of longlining at different times of day would support this view because sockeye and pinks took bait most readily at dawn. Thus, despite the use of different fishing methods to catch salmon in the two seasons, presumably the observations on feeding are for similar periods within their diurnal feeding cycle. Unknown, however, is the selective action of the two gears for feeding fish in different seasons. For the purpose of this paper, for the sizes of fish available to each gear, no significant difference in selectivity is assumed.

The numbers of sockeye and pinks with and without food in their stomachs during these two seasons and the mean quantity of ingested material, based only on fish with food, are presented in Table II. Although mean values for January are in cubic centimeters and those for May–June are in grams, these units are considered equal measures of capacity. Also, for each species, these values are unadjusted for fish size since the quantity of contents was not significantly correlated with fish size (length) (for sockeye, $r = 0.25$, $n = 682$; for pinks, $r = 0.17$, $n = 197$.).

TABLE II. Percentages of feeding sockeye and pink salmon and mean quantity of stomach contents during winter and early summer. Data for early summer are from LeBrasseur (1965). (Numbers of fish examined given in parentheses.)

	% with food		Mean quantity (fish with food)	
Species	Winter	Early summer	Winter (*cc*)	Early summer (g)
Sockeye	50(87)	86(601)	4.6(44)	8.5(517)
Pink	62(24)	90(175)	3.5(15)	8.3(158)

Two points emerge from a comparison of the data in Table II. First, on the basis of chi-square tests for homogeneity, for each species the numbers of feeding fish in the two seasons differed significantly (for sockeye, $\chi^2 = 63.15$, $P < 0.01$; for pinks, $\chi^2 = 14.64$, $P < 0.01$). Second, on the average, fish in early summer contained almost twice the quantity of food in their stomachs as fish in winter. Thus, it can be concluded that sockeye and pinks feed more intensively in early summer than in winter. Whether this reflects seasonal differences in availability or abundance of food or in relative activity of the salmon cannot be answered by these data.

Andrievskaya (1957) and Allen and Aron (1958), studying food of salmon in the northwest Pacific Ocean in spring and summer, showed for the three major species — sockeye, pink, and chum — qualitative differences in the diet of fish inhabiting different areas. LeBrasseur (1966) in his studies also showed spatial differences in the relative importance of food organisms in the summer diet of salmon in the northeast Pacific Ocean, but further pointed out that these differences were largely associated with oceanographic domains.

Since sockeye and pinks in the northeast Pacific Ocean differ seasonally in their geographic distribution (Anon., 1964; Manzer et al., 1965) and, depending on the time of year, may inhabit more than one domain, seasonal differences in the diet of these species were determined by comparing stomach contents of fish from similar domains (Table III). The domains considered are subarctic for sockeye and transitional for pinks, since in winter virtually all fish of the respective species were caught in these domains (Manzer and Dodimead, MS, 1965; Anon., 1966).

Notable qualitative differences in the diet of these species in winter and early summer are also indicated. For sockeye, fish were dominant in winter, accounting for 71% of the total food ingested. In early summer, in contrast, squid were most important. With pinks, amphipods were most important in winter, constituting almost all of the stomach contents. In early summer, euphausiids were most important (44%), followed by amphipods (34%).

From the foregoing it can be concluded that the food ingested by sockeye and possibly pink salmon in winter and in early summer differed both in quantity and quality.

TABLE III. Percentage composition of food of sockeye salmon in the subarctic domain and pink salmon in the transitional domain in the northeast Pacific during winter and early summer seasons. Data for early summer are from LeBrasseur (1966).

	Sockeye		Pink	
Organism	Winter	Early summer	Winter	Early summer
Amphipod	1	3	97	34
Copepod	–	<1	–	4
Euphausiid	<1	<1	1	44
Pteropod	–	–	–	7
Squid	27	88	<1	–
Fish	71	4	1	2
Miscellaneous + unidentified	1	5	<1	9
No. of fish examined	87	187	24	16

The author acknowledges the assistance of the Nanaimo Station's Scale Reading and Computer Service Groups and Messrs C. E. Turner and L. W. Barner, who carried out, frequently under difficult physical conditions, the various field routines which were part of this study. Dr R. R. Parker and Mr R. J. LeBrasseur helpfully commented on the manuscript.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

J. I. MANZER

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REFERENCES

ALLEN, G. H., AND W. ARON. 1958. Food of salmonid fishes of the western North Pacific Ocean. U.S. Fish Wildlife Serv., Spec. Sci. Rept. No. 237. 11 p.

ANDRIEVSKAYA, L. D. 1957. [The food of Pacific salmon in the northwestern Pacific Ocean.] Materialy po Biologii Morskovo Perioda Zhigni Dalnevostochnykh Lososei. p. 64–75. (In Russian.) (Transl. Fish. Res. Bd. Canada, No. 812.)

ANON. 1964. International North Pacific Fisheries Commission, Annual Report for 1962.
1966. International North Pacific Fisheries Commission, Annual Report for 1964.

LEBRASSEUR, R. J. 1965. Stomach contents of salmonids caught in the northeastern Pacific Ocean — 1958. Fish. Res. Bd. Canada, Pacific Biol. Sta. Circ., Statist. Ser., No. 15.
1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Bd. Canada, **23**(1): 85–100.

MANZER, J. I., AND A. J. DODIMEAD. MS, 1965. Winter distribution of salmon in the northeast Pacific Ocean, January 7–February 7, 1964, with some reference to oceanographic conditions. Fish. Res. Bd. Canada, MS Rept. (Biol.), No. 824. 16 p.

MANZER, J. I., T. ISHIDA, A. E. PETERSON, AND M. G. HANAVAN. 1965. Salmon of the North Pacific Ocean — Part V. Offshore distribution of salmon. Bull. Intern. North Pacific Fish. Comm., No. 15. 452 p.

A Method of Obtaining Permanent Dry Mounted Chromosome Preparations from Teleost Fish

McPhail and Jones (1966) reported a technique for obtaining chromosome preparations from the branchial epithelium of teleost fishes. This technique is rapid and simple when compared with older methods which involve the use of embryonic tissues or tissue cultures. As in all previously reported methods, McPhail and Jones make use of aceto-orcein or aceto-carmine as combined stain-fixatives and obtain temporary, wet smears. Wet preparations have the disadvantage of a short useful life, require refrigerated storage, and phase-contrast illumination for examination.

Information from several sources was used in developing the present technique. Darlington and LaCour (1966) give information on techniques of fixation and staining which were employed in this work. Additional information on chromosome staining and mounting was obtained from Parker (1950) and Rothfels and Seminovitch (1958).

The technique reported here has been used successfully for preparing chromosome smears of epithelium from gill filaments and consists essentially of four steps: (1) colchicine treatment; (2) potassium cyanide and triple-distilled water dialysis; (3) acetic acid fixation; (4) Giemsa's stain. Procedural modifications for obtaining metaphase plates of testis, kidney, and blastodisc cells are also noted.

Initial treatment of the fish was similar to that reported by McPhail and Jones (1966). The fish was given a 0.01–0.02-cc dorsal intra-muscular injection of 0.01% colchicine and allowed to incubate under heavy aeration for 2–6 hr at 16–20 C. Optimum incubation time for testis and kidney cells was 12–20 hr. In the preparation of blastodisc smears, no colchicine was used. Fertilized eggs of *Culaea inconstans* were incubated for 36 hr at 18 C and the smears were prepared directly.

After incubation, the fish was killed by pithing. For gill epithelial preparations, the 4th branchial arch was removed and placed in fish Ringer's solution. All mucous, blood, and other debris adhering to the gill lamellae were removed with needlepoint forceps. Excised testis and kidney were minced with corneal scissors into pieces 1–2 mm diam. In the case of blastodiscs, all yolk material was removed from the cells.

After cleaning, the gill arch, minced testis, or kidney was transferred by forceps or pipette to a watch glass containing 0.1 M KCN for a period of 20–90 sec, depending on the size of the arch or pieces of tissues. Larger arches required more time in KCN. During this interval, the action of the KCN could frequently be noted by a "twitching" of the filaments which indicated a successful disruption of the osmoregulatory mechanism of the epithelial cells and subsequent inflow of solution. Minced testis and kidney tissues did not show this

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reaction, but good results were obtained using the same duration of treatment. It was not necessary to precede the dialysis of blastodisc cells with KCN treatment.

The KCN-treated arch was immediately transferred to another watch glass containing triple glass-distilled water for 3–5 min or until the filaments were visibly swollen. The dialysis of testis may require as much as 15 min. When the KCN treatment was omitted, dialysis of gill filaments in triple-distilled water required at least 30 min and was found not to produce good metaphase spreads as frequently as when pre-treated with KCN. Cleaned blastodiscs were transferred from Ringer's directly to a drop of triple-distilled water on a slide. Good results were obtained with 10 min of dialysis.

After dialysis, the tissues were fixed in 45% acetic acid for 15 min. The fixative is apparently critical to the success of the preparation. Clark's fixative (3:1 ethanol–acetic acid), 70% ethanol, and 10% formalin were unsatisfactory. With the first two, the cells either clumped or failed to detach from the gill filaments. With formalin, many nuclei were destroyed. Various concentrations of acetic acid were also tried unsuccessfully in an attempt to obtain better spreading of the chromosomes and distribution of the cells when smearing. Nuclear destruction was evident at concentrations below 35% and chromosomes clumped at concentrations over 50%.

Immediately after fixation, a monolayer of cells was prepared by "painting" the tips of gill filaments across a clean glass slide. Gentle shaking was sometimes required to detach the cells from the gill filaments. A smear of fixed testis or kidney was prepared by placing one or two pieces in a drop of fixative on a glass slide and dispersing it by pressure with the flat side of a clean scalpel blade. Blastodisc cells were dispersed by the fixative alone, and fixation and smearing were done simultaneously in a drop of fixative placed on a slide.

The smear was allowed to air dry and then stained for 1 hr in a working solution of Giemsa's stain. (Giemsa's stock solution: 1 g crystalline Giemsa's stain, 33 ml glycerine, 33 ml methanol. Working solution: 5 ml stock to 100 ml water.) The stained slides were rinsed in distilled water and allowed to dry after which they were mounted with Permount mounting medium.

Smear obtained by the method reported here have shown no deterioration after 12 months of storage. They have the further advantages of yielding nuclei which are almost always flat enough to be included within the depth of focus of an oil immersion objective and which have undergone none of the mechanical disruption involved in squashing techniques. The density of staining provides ample contrast for examination and photography with brightfield illumination.

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Department of Zoology
University of Manitoba, Winnipeg, Man.

KENNETH W. STEWART
CATHERINE B. LEVIN

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REFERENCES

DARLINGTON, C. D., AND L. F. LACOUR. 1966. The handling of chromosomes. 4th revised ed., 6th printing. George Allen and Unwin, Ltd. London. 263 p.

MCPHAIL, J. D., AND R. L. JONES. 1966. A simple technique for obtaining chromosomes from teleost fishes. J. Fish. Res. Bd. Canada, **23**: 767–769.

PARKER, RAYMOND, C. 1950. Methods of tissue culture. Paul B. Hoeber, New York. xv + 294 p.

ROTHFELS, K. K., AND L. SEMINOVITCH. 1958. An air drying technique for flatterning chomosomes of mammalian cells grown *in vitro*. Stain Technol., **33**: 73–77.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

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1227. ACKMAN, R. G., C. A. EATON, AND S. N. HOOPER. 1968. Lipids of the fin whale (*Balaenoptera physalus*) from North Atlantic waters. IV. Fin whale milk. Canadian J. Biochem., **46**: 197–203.

1228. ACKMAN, R. G., AND S. N. HOOPER. 1968. Examination of isoprenoid fatty acids as distinguishing characteristics of specific marine oils with particular reference to whale oils. Comp. Biochem. Physiol., **24**: 549–565.

1229. SHIEH, H. S. 1968. Enzymatic oxidation of ^{14}C-labelled betaine by the marine microbe *Achromobacter cholinophagum*. Canadian J. Biochem., **46**: 21–23.

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